UNIVERSITÉ DU QUÉBEC À MONTRÉAL

COMPORTEMENT ALIMENTAIRE DE LA LIVRÉE DES FORÊTS (*MALACOSOMA DISSTRIA* HÜBNER) SUR QUATRE DE SES PLANTES HÔTES.

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AVANT-PROPOS

J'ai été la principale personne à effectuer les expériences décrites dans ce mémoire. J'ai également été l'auteur principal de l'article et de la note inclus dans ce mémoire. Le deuxième auteur est Yves Mauffette. L'article et la note sont à soumettre.

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RÉSUMÉ

La livrée des forêts (*Malacosoma disstria* Hbn.) est un défoliateur épidémique très connu en Amérique du Nord. Lors d'épidémies, l'éventail des plantes qu'elle consomme s'élargit considérablement mais la façon dont l'insecte se comporte face à cette hétérogénéité reste peu connue. L'objectif de cette étude est de comparer le comportement de chenilles de livrée des forêts lors de leur consommation de feuillage d'espèces différentes. Il s'agit également d'évaluer l'effet de l'âge des larves et de leur expérience alimentaire sur ce comportement et d'en évaluer les conséquences sur la biologie de l'insecte. Un total de 111 chenilles ont été filmées en laboratoire alors qu'elles s'alimentaient d'une feuille de peuplier faux-tremble (*Populus tremoloides*), d'érable à sucre (*Acer saccharum*), de bouleau blanc (*Betula papyrifera*) ou de chêne rouge (*Quercus rubra*). Leurs activités (consommation, déplacement, pauses) ont été enregistrées durant une heure. Leur taux de consommation durant la période d'observation a aussi été relevé. Les chenilles ont ensuite été suivies durant 24 heures, au terme desquelles leur taux de consommation, ainsi que leur efficacité d'utilisation de la nourriture ont été calculés. On observe deux patrons d'alimentation distincts lorsque l'insecte s'alimente d'hôtes primaires versus secondaires. Sur l'érable et le chêne, des hôtes secondaires, les chenilles s'alimentent de façon discontinue et ce, sur le pourtour de la feuille. De manière générale, elles allouent le même temps à la consommation. Elles consacrent cependant plus de temps aux déplacements que sur le peuplier ou le bouleau. Sur le peuplier et le bouleau, en revanche, leur consommation est peu interrompue et très ciblée et elles allouent plus de temps aux pauses que sur leurs hôtes secondaires. Malgré cette différence de comportement, les taux de consommation restent similaires sur les différentes espèces. Ces résultats indiquent qu'une espèce généraliste telle que la livrée des forêts démontre une flexibilité dans son comportement alimentaire, ce qui peut être un atout face à l'hétérogénéité nutritionnelle à laquelle elle est confrontée. Ils indiquent cependant que sur des hôtes secondaires, ces changements de comportement peuvent engendrer des coûts additionnels à ceux de la déficience nutritive.

Mots-clés : comportement alimentaire, budget d'activités, polyphagie, Lepidoptères, *Malacosoma disstria*, *Populus tremuloides*, *Acer saccharum*, *Betula papiryfera*, *Quercus rubra*.

CHAPITRE I – INTRODUCTION GÉNÉRALE

1.1. Problématique

De manière optimale, la quête alimentaire des insectes phytophages devrait maximiser le gain de nutriments tout en minimisant les risques pour la survie de l'animal (Hassel et Southwood, 1978). La qualité de la nourriture est essentielle à la performance biologique des herbivores et des feuilles contenant de grandes quantités de protéines et de glucides augmentent fortement la croissance des larves herbivores (Scriber et Slansky, 1981; Fortin, 1994). Bien que les protéines soient considérées comme le nutriment le plus important pour la croissance car elles constituent la matière première pour la fabrication de nouveaux tissus, un équilibre entre protéines et glucides est nécessaire car ces derniers constituent la source d'énergie nécessaire à cette croissance (Lindroth et Bloomer, 1991, Simpson *et al.*, 1995). Les insectes herbivores devraient donc être en mesure de sélectionner le feuillage de meilleure qualité en fonction de leurs besoins nutritionnels (Simpson, 1990; Simpson *et al.* 1995). Confrontés à une ressource hétérogène aux échelles spatiale, temporelle ou chimique comme le sont les végétaux, ils ont donc développé des réponses comportementales modulables afin d'optimiser les gains en nutriments et de limiter les coûts associés à leur quête alimentaire (Schultz, 1983; Bernays et Chapman, 1994).

L'étendue des hôtes des insectes phytophages, résultat de leur coévolution avec les divers groupes de plantes, varie considérablement d'un groupe d'insectes à un autre (Dethier, 1982). La plupart d'entre eux sont très spécifiques dans le choix de leurs hôtes (Jaenike, 1990 ; Bernays et Chapman, 1994). Dans l'Ordre des Lépidoptères, environ 55% des espèces ne se nourrissent que d'un seul genre de végétaux, 30% se nourrissent d'une seule famille de végétaux et 15% se nourrissent de plus d'une famille (Bernays et Chapman, 1994).

Le questionnement concernant l'étendue des hôtes sur lesquels une espèce se nourrit (spécialiste versus généraliste) constitue une des problématiques les plus

intéressantes de l'étude de l'écologie des insectes. Pourquoi existe-t-il des insectes phytophages dont l'alimentation s'étend à des plantes provenant de plusieurs familles, les polyphages, et d'autres, la plus grande partie d'entre eux, dont l'alimentation est restreinte à une seule espèce ou à quelques espèces d'une même famille, les monophages et oligophages respectivement (selon les définitions de Bernays et Chapman, 1994) ?

Cette question a été l'objet d'un bon nombre d'études visant à expliquer l'origine et le maintient de la diversité parmi les insectes (ex. Jaenike, 1990). Bien que les théories explicatives du phénomène de spécialisation de l'alimentation abondent également (Futuyma et Moreno, 1988 ; Jaenike, 1990 ; Bernays et Chapman, 1994, en donnent des exemples), il semblerait qu'un ensemble de facteurs en interactions soient à prendre en considération et qu'aucune règle unique ne soit applicable à l'ensemble des groupes d'insectes (Bernays et Chapman, 1994). Les pressions de prédation et d'autres aspects de l'habitat jouent certainement un rôle important, mais il semblerait que la chimie des plantes et les processus de traitement de cette information par l'insecte aient une place centrale et seraient le meilleur candidat comme facteur explicatif, commun à tous les insectes, de la spécialisation de l'alimentation (Bernays et Chapman, 1994, Raubenheimer et Simpson, 2003).

Le comportement d'un individu défini une grande partie des pressions de sélection auxquelles il est sujet (Lewontin, 1983). Un changement évolutif de comportement est souvent initiateur de changement de niche écologique et, par exemple, l'acceptation par les insectes phytophages d'une plante introduite, peut-être basée sur des changements évolutifs de comportement sans adaptation physiologique apparente (Futuyma et Moreno, 1988). L'étude du comportement alimentaire de l'animal herbivore, en relation avec ses traits morphologiques, physiologiques, sa performance et son interaction avec la chimie foliaire des plantes est donc cruciale afin d'obtenir une image plus complète de son écologie nutritionnelle et, dans le cas particulier d'une espèce polyphage, afin de mieux comprendre l'évolution et le maintient de l'étendue de ses hôtes.

1.2. Espèce à l'étude : la livrée des forêts, *Malacosoma disstria* Hübner.

Les larves de lépidoptères, et plus particulièrement le genre des chenilles à tente (*Malacosoma spp.*) représentent un bon outil pour des études sur le comportement alimentaire d'insectes phytophages (Dethier, 1987 ; Fitzgerald, 1995). Elles se développent bien en laboratoire et ont été utilisées avec succès afin d'étudier des principes généraux d'histoire de vie et de comportement des lépidoptères grégaires (Fitzgerald, 1995). Certaines espèces de cette famille sont réputées pour leurs périodes épidémiques dévastatrices, et c'est à des fins de contrôle de ces invasions qu'un certain nombre d'études se sont intéressées à la croissance, au développement ainsi qu'au comportement de ces espèces, depuis plus d'une centaine d'années (Dyar, 1890 ; Britt, 1970 ; Fitzgerald, 1995 ; Nicol *et al.*, 1997). La livrée des forêts fait partie de ces espèces épidémiques particulièrement dévastatrices; elle est d'ailleurs la plus répandue dans le genre des chenilles à tente (Fitzgerald, 1995).

C'est un lépidoptère printanier qui n'a qu'une génération par année (Stehr et Cook, 1968). Les larves herbivores éclosent au début du printemps (en général début à mi-mai), en étroite synchronie avec les premières feuilles de leur hôte natal (Fitzgerald, 1995). Elles ont alors un comportement grégaire, tout au moins aux premiers stades de la larve (Fitzgerald et Costa, 1986). On rapporte 5 ou 6 stades de développement en nature pour les larves de livrées des forêts (Hodson, 1941 ; Muggli et Miller, 1980 ; Smith *et al.*, 1986 ; Fitzgerald, 1995), mais on a pu en dénombrer jusqu'à 8 en laboratoire, sur une diète artificielle (Etilé et Despland, 2008). Elles atteignent la maturité vers la mi-juillet et pupent à l'intérieur de cocons de soie qu'elles fabriquent dans des feuilles enroulées. L'adulte éclot environ 10 à 15 jours plus tard, se reproduit et meurt peu de temps après que les femelles aient pondu leurs œufs autour de petites branches. Les larves pharates entrent alors en diapause jusqu'au printemps suivant (Fitzgerald, 1995).

La livrée des forêts est probablement la plus généraliste des espèces de chenilles à tente (Fitzgerald, 1995). Les livrées peuvent se nourrir de feuillage de peuplier faux-tremble (*Populus tremuloides*), bouleau à papier (*Betula papyrifera*),

érable à sucre (*Acer saccharum*), nyssa sylvestre (*Nyssa sylvatica*), tilleul d'Amérique (*Tilia americana*) ou chêne rouge (*Quercus rubra*). Lors de périodes épidémiques, ce spectre peut s'étendre à bien d'autres espèces comme le chêne à gros glands (*Quercus Macrocarysa* Michx.), le frêne vert (*Fraxinus pensylvanica*), le mélèze (*Larix* spp.), divers types de fleurs et autres noisetiers, fraisiers, agrumes, pois, choux, betteraves ou pommes de terre selon leur emplacement géographique (Hodson, 1941 ; Fashingbauer *et al.*, 1957 ; Stehr et Cook, 1968 ; Fyre et Ramse, 1975 ; Fitzgerald, 1995 ; Nicol *et al.*, 1997). Des défoliations importantes ont même été rapportées sur une espèce qui était jusqu'alors considérée comme totalement inacceptable par la livrée des forêts : l'érable rouge (*Acer rubra*) (Fitzgerald, 1995 ; Wink et Allen, 2007).

Malgré cette grande diversité dans son alimentation, la livrée des forêts montre tout de même des préférences pour certaines essences forestières. Au Québec, l'hôte principal de la livrée des forêts est le peuplier faux-tremble (*Populus tremuloides*). Le bouleau blanc (*Betula papyrifera*) est aussi considéré comme un de ses hôtes principaux dans la région. Une étude menée vers la limite Nord de l'insecte dans la province (Lareau, 1997), a montré qu'aucune différence n'était notable dans la performance des livrées qu'elles soient sur du peuplier faux-tremble (*Populus tremuloides*) ou du bouleau blanc (*Betula papyrifera*). Théoriquement, le succès d'un insecte devrait être supérieur sur son hôte primaire qu'il ne l'est sur des hôtes secondaires (Hough et Pimentel, 1978). Les études de Lorenzetti (1993), Trudeau (1997) et Nicol *et al.* (1997), confirment cette théorie pour la livrée des forêts. Sa performance biologique (temps du développement larvaire, taux de croissance larvaire, poids des chrysalides et survie) est meilleure sur le peuplier faux-tremble que sur l'érable à sucre. Le feuillage du peuplier faux-tremble serait de meilleure qualité nutritive que celui de l'érable à sucre et ceci serait attribuable au fait que le peuplier contient environ deux fois plus de sucres solubles et l'érable plus de phénols totaux (composés secondaires de défense et/ou inhibiteurs de croissance) (Lorenzetti, 1993 ; Nicol *et al.* 1997, Fortin *et al.*, 1999 ; Panzuto *et al.*, 2001). L'érable à sucre

reste tout de même un des principaux hôtes des larves de livrée au sud du Québec, qui s'orientent préférentiellement vers les feuilles de lumière plutôt que vers les feuilles d'ombre de cet hôte (Panzuto *et al.*, 2001). Cette préférence se reflète également sur la performance des individus, supérieure sur les feuilles de lumière (Fortin et Mauffette, 2002).

Plusieurs études se sont donc penchées sur l'effet de la qualité de l'hôte sur la performance biologique de la livrée des forêts et ont montré une augmentation de cette performance sur les hôtes nutritionnellement supérieurs, et préférés de la livrée (Lorenzetti, 1993 ; Trudeau, 1997 ; Nicol *et al.*, 1997 ; Lévesque *et al.*, 2002). Cependant, ces études s'intéressent peu ou pas à l'aspect comportemental des insectes confrontés à ces différentes sources de nourriture. L'une d'entre elles (Lévesque *et al.*, 2002) montre que chez la livrée des forêts, la quantité de nourriture ingérée ainsi que le taux de consommation relatif tout au long d'un stade larvaire sont supérieurs sur une nourriture de qualité nutritive supérieure, ce qui contribuerait à l'augmentation de performance des larves. Ceci indiquerait donc que le comportement alimentaire de la livrée des forêts constitue une composante majeure de son écologie nutritionnelle et que son étude à différentes échelles devrait permettre de mieux comprendre comment cette espèce est capable de composer avec la variabilité existant dans son alimentation. L'importance de l'étude du comportement des individus afin de comprendre un mode de vie polyphage a été démontrée pour plusieurs autres espèces d'insectes, de mammifères et d'oiseaux (Singer and Bernays, 2003).

1.3. Comportement alimentaire des insectes phytophages

L'acceptation ou le rejet de plantes par les insectes phytophages dépend de leurs réponses physiologiques face aux caractéristiques de la plante, ces caractéristiques pouvant être physiques ou chimiques. Les caractères morphologiques des plantes peuvent influencer l'acceptabilité soit en fournissant des informations visuelles, soit en agissant sur la capacité des insectes à mordre dans le feuillage

(Feeny, 1976 ; Bernays et Chapman, 1994). Les caractères chimiques peuvent influencer le choix d'hôtes des insectes de diverses façons. Tout d'abord, les chenilles sont capables de détecter les composés chimiques volatiles des plantes à distance grâce aux sensilles situées sur leurs antennes (Fitzgerald, 1995). La distance jusqu'à laquelle les chenilles de livrées des forêts sont capables de détecter ces composés chimiques n'est cependant pas déterminée. Ces sensilles olfactives ont également un rôle dans la phase finale d'acceptation de la plante car elles peuvent aussi servir à discerner les composés chimiques volatiles se situant très près de la surface de la feuille. La composition chimique de la surface de la feuille (couche de cire couvrant la feuille) semble aussi avoir un rôle dans l'acceptation de la plante par les insectes. Ils sont capables de caractériser cette cire grâce à des chimiorécepteurs de contact situés sur leur tarse et leurs parties buccales (Bernays et Chapman, 1994). Ce caractère semble être particulièrement utile aux adultes de certaines espèces qui ne sont pas en mesure de tester la chimie à l'intérieur des feuilles, afin de choisir leur hôte d'oviposition (Chapman, 1982). La dernière phase dans le processus aboutissant à l'acceptation ou au rejet de la nourriture par l'insecte est l'évaluation de la chimie interne des feuilles. Lorsqu'un insecte mord dans une feuille, le contenu des cellules est libéré et les chimiorécepteurs de contact des parties buccales sont alors stimulés par les composés chimiques de la feuille. Parmi ces composés, certains seront phagostimulants, d'autres vont repousser les insectes ou les dissuader de manger, et ce sont les informations reçues de ces composés qui vont en partie déterminer le comportement des insectes durant un repas, après avoir été traitées par le système nerveux central (Simpson, 1995 ; Simpson, Raubenheimer et Chambers, 1995). Les principaux phagostimulants pour les insectes phytophages sont les nutriments, et plus particulièrement les sucres (le fructose et le saccharose étant considérés comme étant les plus phagostimulants). L'effet stimulant des protéines est moindre par rapport à celui des sucres malgré leur grande importance nutritionnelle, mais les insectes sont tout de même capables de détecter certains acides aminés et ceci aurait une influence sur la durée des repas ou la durée des intervalles entre les repas (Bernays et Chapman,

1994). Les composés dissuasifs (ou composés de défense) sont principalement les composés secondaires des plantes. Leur efficacité augmente à mesure que leur concentration augmente par rapport aux éléments phagostimulants (Bernays et Chapman, 1994).

Simpson (1995) donne une explication détaillée des facteurs déterminant la régulation du repas et les comportements qui en découlent. Le moment où le repas commence est déterminé par le niveau d'inhibition résultant des précédents repas, l'excitation générée par la présence de nourriture et d'autres facteurs comme le fait que l'insecte vienne de déféquer, son rythme interne, les conditions environnementales ou la présence d'autres individus. Si le niveau d'excitation de l'insecte excède le seuil d'alimentation, le repas commencera. Une fois le repas initié, un input gustatif soutenu est nécessaire afin qu'il continue. Trois paramètres définissent alors un repas : la quantité ingérée, la durée du repas et le taux de consommation durant le repas. Le taux de consommation serait une fonction positive du niveau d'excitation mais aussi des propriétés physiques de la nourriture (ex : une feuille tendre est plus facile à consommer qu'une feuille dure). L'amplitude et la durée de l'effet excitant de la nourriture nécessaire à la continuation du repas sont une fonction des propriétés chimiques de la nourriture et de feedbacks provenant du système périphérique tels que des récepteurs d'étirement sur la paroi intestinale, des hormones ou encore la teneur en nutriments de l'hémolymphe. Le repas s'arrête lorsque ces feedbacks négatifs qui augmentent tout au long du repas excèdent les niveaux d'excitation présents au début et durant le repas (Simpson, 1995).

1.4. Facteurs pouvant influencer le comportement au moment de l'alimentation

1.4.1. Âge de la larve

Les besoins nutritionnels d'un insecte changent au long de leur développement et ces changements se reflètent par des variations dans le comportement alimentaire durant le développement (revu dans Barton Browne,

1995 ; Barton Browne et Raubenheimer, 2003). Il existe cependant très peu d'information sur les mécanismes comportementaux associés à la quête de nutriments à différents stades larvaires. Ces changements comportementaux pourraient inclure des variations dans la durée des repas, dans la durée de l'intervalle entre les repas, dans la proportion de temps que l'insecte consacre à la consommation au sein d'un repas, et/ou dans le taux de consommation instantané (Simpson, 1990). Les études où ces variables ont été mesurées considèrent, à peu d'exceptions près, qu'elles sont ontogénétiquement fixe en ne les observant que sur une étroite fenêtre du développement et/ou en les compilant sur toute la période d'observation, quel que soit le nombre de stades larvaires traversés. En ce qui concerne les larves de lépidotpères, seuls Raubenheimer et Barton Browne semblent s'être penchés sur la question (Raubenheimer et Barton Browne, 2000 ; Barton Browne et Raubenheimer, 2003). Ils rapportent une augmentation du taux d'ingestion et de la taille des repas au cinquième stade par rapport au quatrième de la chenille *Helicoverpa armigera*. Malheureusement, aucun détail des activités alimentaires telles la consommation, les déplacements ou encore le repos n'ont été analysés dans cette étude.

Chez la livrée des forêts, le quatrième stade correspond au moment où la grégarité devient moins importante pour les larves et où elles commencent à chercher leur nourriture de manière indépendante (Fitzgerald, 1995). À partir de ce stade, la thermorégulation et les repères apportés par le comportement grégaire des plus jeunes serait moins vital aux chenilles (Fitzgerald, 1995 ; Despland et Hamzeh, 2004). Le cinquième stade, quant à lui, est celui auquel les livrées consomment 82.2% de la consommation totale de leur vie et dans la plupart des cas observés en nature, le dernier stade larvaire (Fitzgerald, 1995). Les besoins nutritionnels d'une chenille au stade 5 étant alors supérieurs à ceux d'une chenille de stade 4, on peut alors supposer que des stratégies alimentaires variables seraient associées à cette différence de besoins.

1.4.2. Expérience alimentaire

Plusieurs études montrent que l'expérience et l'apprentissage jouent également un rôle non négligeable dans le comportement des insectes (Bernays et Chapman, 1994 ; Simpson et Raubenheimer, 1996). Les réponses nutritionnelles associées à l'expérience chez les insectes phytophages incluent des réponses associatives (l'animal apprend à associer un stimulus n'ayant aucun effet notoire à un stimulus ayant un effet positif ou négatif) et des réponses non-associatives telles que la néophilie (préférence pour une nouvelle alimentation) ou l'induction de la préférence (préférence pour une alimentation déjà expérimentée, quelle que soit sa valeur nutritionnelle) (Bernays et Chapman, 1994 ; Simpson et Raubenheimer, 1996). Il est alors possible que ces phénomènes soient capables d'influencer le comportement des livrées des forêts au moment de leur alimentation.

Par ailleurs, afin de satisfaire leurs besoins nutritionnels à partir de sources alimentaires dont la concentration en nutriments est variable, certaines espèces sont capables de réguler la consommation de ces différents nutriments essentiels indépendamment les uns des autres (Simpson *et al.* 1995). Ceci a été démontré pour plusieurs insectes généralistes lépidoptères (*Manduca sexta* (Thompson et al. 2001), *Spodoptera littoralis* (Simpson *et al.*, 1988a), *Heliotis zea,* (Schiff *et al.*, 1989; Friedman *et al.*, 1991), *Anticarsia gemmatalis*, (Slansky et Wheeler, 1989)) ou orthoptères (*Locusta migratoria* (Simpson *et al.*, 1988b; Raubenheimer et Simpson, 1993)), sur une nourriture artificielle. Des individus nourris d'une nourriture déficiente en un nutriment (protéines ou glucides), pouvait ensuite compenser pour ce manque en s'orientant préférentiellement vers une nourriture riche en ce nutriment.

1.4.3. Hôte présent

L'étude du comportement d'approvisionnement de la livrée des forêts sur des arbres artificiels de composition variable a montré que celui-ci était influencé par la présence de son hôte préférentiel, le peuplier faux-tremble (Drouin, 2007). En effet, lorsque des feuilles de peuplier étaient présentes sur les arbres artificiels composés

d'érable à sucre, les chenilles se reposaient davantage qu'elles ne se déplaçaient et le contraire était observé en leur absence. Elles avaient également tendance à orienter leur consommation vers les feuilles de peuplier plutôt que celles d'érable à sucre (Drouin, 2007).

1.5. Utilisation post-ingestive de la nourriture

Les insectes phytophages doivent traiter de grandes quantités de nourriture parce qu'ils ne sont capables d'assimiler qu'une petite partie de toute l'énergie qui se trouve dans les feuilles (Hemmings and Lindroth, 1995). Ces feuilles sont en majeure partie constituées de composés non digestibles tels la cellulose et la lignine qui passent à travers le tube digestif sans être absorbés et qui sont ensuite éliminés dans les excréments. De plus, de cette quantité d'énergie assimilable, une partie sera utilisée pour la respiration, la soie, ou perdue dans les exuvies, au détriment d'un investissement dans la croissance ou dans la reproduction. L'efficacité qu'ont les insectes à utiliser l'énergie disponible dans les feuilles peut être mesurée à l'aide de plusieurs indices, initialement décrits par G.P. Waldbauer (1968) :

- la proportion de nourriture ingérée qui est effectivement digérée constitue *l'efficacité d'assimilation* (AD pour « approximate digestibility »)

- la proportion de nourriture ingérée effectivement convertie en biomasse constitue *l'efficacité de conversion de nourriture ingérée* (ECI pour « efficiency of conversion of ingested food »)

- la proportion de nourriture digérée effectivement convertie en biomasse constitue *l'efficacité de conversion de nourriture digérée* (ECD pour « efficiency of conversion of digested food »).

Un concept central à l'écologie nutritionnelle est que l'ingestion et l'utilisation de la nourriture sont des processus dynamiques que les organismes peuvent ajuster de manière adaptative en réponse à leurs besoins, ce qui leur permet de s'approcher d'un taux de croissance optimal, même lorsque la qualité de la nourriture en présence est très variable (Slansky et Rodriguez, 1987). Dans le cas de la livrée des forêts, une

analyse de l'effet de la qualité de la nourriture sur l'efficacité d'utilisation de celle-ci a montré que l'efficacité d'assimilation (AD) et l'efficacité de conversion de nourriture ingérée (ECI) étaient supérieures sur du feuillage de qualité nutritive supérieure (Lévesque *et al.*, 2002).

1.6. Objectif et hypothèses

La plupart des études explorant la quête alimentaire chez les insectes phytophages se sont concentrées sur les préférences, les réponses physiologiques ou la performance des individus en fonction de la qualité de leurs hôtes. Certaines études, dites comportementales des insectes ont observé ce comportement alimentaire en terme de quantité de nourriture ingérée. Les changements dans les activités des individus au moment de la consommation de cette nourriture ne sont que très peu décrits pour la livrée des forêts. Ces changements comportementaux pourraient être influencés par l'état d'excitabilité centrale des individus, par leur génétique, par leur stade de développement mais aussi par leurs expériences passées d'alimentation. Selon la qualité de la nourriture consommée, ces changements comportementaux pourraient inclure des variations dans :

- le temps alloué aux déplacements, à la consommation ou aux pauses sur une période donnée;
- la fréquence des différents épisodes de déplacement, consommation ou pauses durant cette période ;
- la durée moyenne de ces trois activités.

L'objectif de cette étude est de faire le lien entre la préférence alimentaire des livrées des forêts et leurs patrons de consommation à l'échelle d'un repas sur des feuilles de qualité nutritive variables. Les temps et fréquence des déplacements, consommation et pauses des chenilles de livrées seront comparés sur différentes essences foliaires qui font partie de leurs hôtes d'alimentation. Le comportement post-ingestif des individus sera observé en calculant des indices d'efficacité d'utilisation de la nourriture.

Tout d'abord, nous émettons l'hypothèse que les individus observés sur leurs hôtes secondaires auront tendance à diminuer leur taux de consommation relatif, ce qui, au niveau comportemental, pourrait se traduire par une augmentation des déplacements et une diminution de la consommation, par rapport à leur hôte primaires. Deuxièmement, nous attendons une réponse différente pour des individus de stade 4 versus stade 5, à cause entre autres, de la différence entre les besoins nutritionnels des individus de ces deux stades. Les besoins supérieurs des individus de stade 5 pourrait alors les pousser à augmenter leur temps de consommation au dépens du temps de déplacement et/ou à augmenter leur taux de consommation instantané. Troisièmement, nous croyons que l'expérience alimentaire des individus pourrait influencer leurs réponses comportementales. Une éventuelle aversion face à une nourriture inconnue pourrait alors réduire le taux de consommation des larves, et s'exprimer par une augmentation des déplacements et une diminution de la consommation et du repos. Finalement, conformément à la littérature, nous nous attendons à ce que l'efficacité d'utilisation de la nourriture par des larves de livrées des forêts soit supérieure sur ses hôtes primaires.

CHAPITRE II – FEEDING BEHAVIOUR OF THE FOREST TENT CATERPILLAR, *MALACOSOMA DISSTRIA* HÜBNER ON TREMBLING ASPEN (*POPULUS TREMULOIDES* MICHX.) AND SUGAR MAPLE (*ACER SACCHARUM* MARSH.) LEAVES.

Elsa Etilé and Yves Mauffette

2.1. ABSTRACT

The forest tent caterpillar (*Malacosoma disstria* Hübner (Lep.: Lasiocampidae)) is a major polyphagous pest of North-American deciduous forests. This insect feeds in spring on many different tree species and epidemics can lead to severe defoliation. Few studies have considered the influence of host type on the behaviour of larvae, but some have shown that their daily foraging patterns could be influenced by the type of diet available. Through video-recorded observations, we evaluated and compared foraging behaviours (feeding, movement and pauses) and feeding efficiency of *M. disstria* larvae feeding on trembling aspen (*Populus tremuloides* Michx) and sugar maple (*Acer saccharum* Marsh.). We also evaluated the influence of feeding experience and age of the larvae on their foraging behaviour. Host type, larval age and prior feeding experience affected the behaviour of *M. disstria*. Larvae spent more time moving and less time feeding on sugar maple whereas they fed more continuously on trembling aspen. This resulted in two different feeding patterns of the leaves. They were also more aversed by a host they had never experienced before and 4th instars spent about twice as much time feeding as 5th instars. It is therefore clear that a polyphagous species such as the forest tent caterpillar does not feed in equivalent ways on different hosts and that their feeding behaviour can further be influenced by factors both endogenous and exogenous to the insect. We explore how such plasticity in feeding behaviour could be a valuable asset for a polyphagous way of life and consider the costs associated to changes in feeding behaviour.

Key words: feeding behaviour, activity bouts, time budgets, polyphagy, Lepidoptera, *Malacosoma disstria*, *Populus tremuloides*, *Acer saccharum*.

2.2. INTRODUCTION

Phytophagous insects should have evolved to select the best quality food within the limitation of their nutritional needs and environmental constraints (Simpson, 1995). High heterogeneity in plant food sources have led them to variable feeding strategies which optimize nutritional intake and limit the costs associated with foraging (Hassel and Southwood, 1978; Schultz, 1983; Bernays and Chapman, 1994).

According to their breadth of diet, insects are classified as either generalists (polyphagous) or specialists (monophagous or oligophagous) species. It is generally argued that while generalist species may be able to take advantage of fluctuating resources, specialists may be more efficient in their use of few resources to which they are especially well adapted (Futuyma and Wasserman, 1981). Polyphagy is of particular interest because it implies that insects have developed specific adaptations allowing them to maintain relatively stable growth rates over a gradient of resource quality (Bernays and Chapman, 1994; Kause *et al.*, 1999).

Most studies investigating ecological implications of polyphagy for herbivorous insects have focused on costs and benefits on their performance (e.g. Schroeder, 1986; Lindroth and Bloomer, 1991; Lindroth *et al.* 1993). However, and as mentioned by Singer and Bernays (2003), uncovering the behavioural aspects underlying polyphagy can also inform us on its ecological causes and consequences. Central to this is the understanding of polyphagous insects' foraging behaviour.

Most herbivore insects' feeding pattern consists of a series of discrete meals separated by non-feeding periods (Simpson, 1995). When the insect makes contact with food, it will feed more or less continuously, for a duration that will change according to its own physiological state and the type of sensory input elicited by the food (Simpson, 1995). The amount of food ingested will be the product of the frequency of feeding periods by the average rate of consumption during those feeding

periods (Simpson, 1995). The associated performance of the insect will be a result of the quality of that food and of the quantity of that food it will ingest, digest and convert to leaving material (Simpson, 1995). Changes in the feeding behaviour of insects can include changes in the duration of meals, in the proportion of time within meals during which the insect is actually feeding, moving or immobile, in the frequency and duration of feeding bouts and pauses within the meal, or in the instantaneous rate of ingestion (Simpson, 1990; Raubenheimer and Barton Browne, 2000).

Several factors, both endogenous and exogenous to the insects, can potentially influence their feeding behaviour. As a consequence, the patterns of feeding displayed will result from all possible interactions between those factors (Wright, Raubenheimer and Simpson, 1999). First, the behaviour displayed can depend on the quality of the food. Kause *et al.* (1999) suggested that changes in food quality induce mainly two different behavioural responses in herbivorous insects. Some species are able to increase consumption on low-quality diets (referred to as nutritional compensation) (Simpson *et al.* 1988a, Schiff *et al.* 1989; Friedman *et al.* 1991, Thompson and Redack, 2001). Others reject a low-quality food and search for higher quality leaves (Schultz, 1983; Edwards *et al.*, 1991; Barker *et al.*, 1995). Second, larval age can also influence the feeding behaviour of phytophagous insects. Individuals increase their food intake with development to satisfy increased nutrient demands for growth and maintenance (reviewed in Barton Browne, 1995). This review indicates that an increased food intake with development is frequently due to an increase in intake per unit of time (consumption rate). However, the description of the behaviour underlying such changes is far from being complete. Third, the feeding behaviour of insects can also depend on their previous feeding experience. When phytophagous insects contact and feed on particular plants, this experience can strongly influence future food intake behaviour, determining the type and quantity of plant material that will be ingested in the future (Bernays and Chapman, 1994). This phenomenon is referred to as induction of preference (Bernays and Chapman, 1994).

A generalist herbivore such as the forest tent caterpillar (*Malacosoma disstria* Hübner; Lepidoptera: Lasiocampidae) is a suitable species to study feeding behaviour in polyphagous species. Its larvae develop well in the laboratory and have been successfully used to study life history principles in lepidopterans. Forest tent caterpillars usually go through 5 or 6 larval instars before pupation (Fitzgerald, 1995). The 4th instar corresponds to the time when gregarity becomes less crucial for larvae survival and when they start to forage individually. It is estimated that the last instar (usually the 5th), is when larvae ingest 82.2% of their whole life food intake and when they gain the maximum of their final weight (Fitzgerald, 1995).

The forest tent caterpillar is a broad generalist able to feed on a wide range of plant taxa (Fitzgerald, 1995). Some degree of species-specific preference is widespread among all groups of polyphagous animals (Hassel and Southwood, 1978) and this applies to the forest tent caterpillar. In Québec, its primary host is trembling aspen (*Populus tremuloides*). Sugar maple (*Acer saccharum*) is a secondary host (Fortin *et al.* 1999). Forest tent caterpillar's performance (total larval development time, pupal mass and survival) is higher on aspen than on sugar maple (Lorenzetti, 1993; Trudeau, 1997; Nicol *et al.* 1997). A higher protein and soluble sugars content in aspen and higher secondary compounds (i.e. phenolic glycosides) content in sugar maple are probably responsible for this nutritional benefit of trembling aspen (Lindroth and Bloomer, 1991; Lorenzetti, 1993; Nicol *et al.* 1997; Fortin *et al.*, 1999; Panzuto *et al.*, 2001).

A study of forest tent caterpillars foraging behaviour over day-long observations revealed that it could be altered by the composition of the artificial trees they were observed on (Drouin, 2007). The insects increased movement and decreased rest on trees composed of non-preferred hosts. In our attempt to understand why and how forest tent caterpillars make particular feeding decisions, we focused on the behaviour of the insect at a smaller spatial and time scale. Short-term behavioural mechanisms of feeding in lepidopterans have rarely been analyzed, although they can give valuable information on the adaptative mechanisms of polyphagous insects.

We observed the insect in presence of one leaf during one hour and compared behaviours on two of its feeding hosts: one primary, trembling aspen (*Populus tremuloides)* and one secondary host, sugar maple (*Acer saccharum*). Using laboratory observations, we asked how diet, age and feeding experience could affect the feeding behaviour of forest tent caterpillars.

First, we hypothesize that insects observed on their secondary host, sugar maple, will exhibit a more exploratory behaviour by increasing moving time. Second, we hypothesize that relative consumption rate of insects will be superior on their primary host, trembling aspen, due to an increased feeding stimulation from that host. Third, we expect to see a different response from fourth and fifth instar larvae, due to a difference in their physiological state. Increased needs in fifth instars might force them to increase their feeding time at the expense of moving time and/or to increase their consumption rate. Fourth, we hypothesize that insects will exhibit varying responses to higher- or lower-quality food according to their prior feeding experience. Their consumption rate might be reduced as a consequence of the aversion behaviour engendered by an unknown food. Finally, we will consider the performance of the insects in relation to its feeding host. According to the literature, we expect to see better larval performance on aspen compared to sugar maple.

2.3. MATERIAL AND METHODS

Laboratory experiments were carried out at the Mont-St-Hilaire research center (45.3°N, 73.0°W) in Québec, Canada, from May to July 2005.

2.3.1. Insects rearing

Forest tent caterpillar egg bands were collected in March 2005 at Wabasca, Alberta (55° 57' 00" N - 113° 50' 00" W) and stored at 4°C until the first trembling aspen leaf buds appeared at the end of April 2005 at the Mont-St-Hilaire research center. Five egg bands were then sterilized in 5.4% sodium hypochlorite for 1 minute and 30 seconds, washed in cold tap water for 5 minutes and then rinsed in 0.06% sodium hypochlorite (Grisdale, 1985). Each band was placed in a numbered plastic container lined with wet paper towel and wax paper and covered with a net. The containers were kept in a growth chamber at 24°C, 50% relative humidity, and under a 16L:8D photoperiod.

Between 50 and 150 individuals emerged from each egg mass, starting on May 3rd, 2005. Because of their natural gregarious behaviour, insects were kept in groups until their 4th instar. Several studies have reported a diminution of performance when gregarious insects are reared individually in the laboratory (Haukioja, 1980; Muggli and Miller, 1980; Stamp and Bowers, 1990). However, after the second molt, groups were divided into sub-groups of about 40 individuals, in order to avoid over-crowded conditions.

From the day of eclosion, caterpillars were fed *ad libitum* with freshly cut leaves, replaced everyday in the morning or twice a day if necessary. Leaf dehydration was prevented by inserting petioles into florist vials filled with distilled water. The larvae were reared on two types of diets. Half were given trembling aspen during the whole rearing period (*Populus tremuloides*; referred to as **A** in the text) and the other half was fed a mix of trembling aspen and sugar maple (*Acer*

saccharum) (**M** in the text). Mixing was ensured by alternating aspen and maple every two days. Mixing food during the whole developmental period controlled for potential effects of learning at different stages on behaviour later on in life (Bernays and Chapman, 1994).

Leaves were selected from a sample of 20 mature trees (DBH > 10 cm) on the St-Hilaire Mountain, within a perimeter of 200m around the research center. The site is part of a mixed temperate forest. They were selected according to their position in the canopy; sun aspen leaves and shade maple leaves were chosen. In a situation of choice, the preference of forest tent caterpillars is: aspen > sun maple > shade maple (Panzuto *et al.*, 2001; Fortin and Mauffette, 2002; Levesque *et al.*, 2002). We expected any behavioural difference to be emphasized on sun-aspen versus shade-maple leaves.

2.3.2. Behavioural observations set-up

Freshly molted 4th and 5th instars were transferred from the rearing containers to a new container and allowed to feed for 48 to 72 hours. Individuals used for observation were then randomly picked among them, put into individual Petri dishes and deprived of food during 12 hours before observation time. A total of 35 fourth and 51 fifth instar larvae were used for behavioural observations.

Figure 1.1 shows the device set-up for behavioural observations. A Petri dish was used as observation chamber. A 2mm-diameter hole was pierced into its wall. A florist vial was glued in front so that a leaf petiole could pass through and be maintained into distilled water as shown on figure 1.1.b. Before each observation, the leaf was cut off a tree, weighed and scanned (Scanner HP Scanjet 4070 Photosmart) for surface area calculations (UTHSCSA Image Tool for Windows®, version 3.00).

After the food deprivation period, caterpillars were measured with a caliper (body length and head capsule widths), weighed with an electronic scale (Sartorius H51; precision: 0.01mg), then placed into one observation chamber.

A digital camera (Sony Handycam, DCR-DVD201) recorded caterpillars' behaviour. The video started once the insect initiated feeding in order to ensure that stress related to manipulation was over by the time the observation started.

An observation consisted in a video record of one caterpillar feeding on a leaf of either trembling aspen (**A**) or sugar maple (**S**) for approximately 60 minutes. Table I summarizes the experimental design for video observations. A total of 86 hours of video were recorded from May, 22nd to July, 5th 2005.

2.3.3. Data collected

2.3.3.1. Ingestive traits

- For the 1-hour observation period

After the 1-hour observation, the leaves were weighed to calculate insects relative consumption rate based on fresh leaf mass (RCR_{fm}). They were then dried at 60°C for 24 hours and weighed again for calculations of relative consumption rate based on dry leaf mass (RCR_{dm}). More individuals were used for consumption evaluation but their behaviour was not recorded. A total of 70 fourth and 75 fifth instar larvae were used for RCR_{dm} calculations.

- For the 24-hours follow-up

The larvae were removed from the observation chamber and put into a new Petri dish for 24 hours with one fresh leaf of the same species they had been filmed on. After this period, the leaf and larva were dried at 60°C for 24 hours and weighed for consumption and performance calculations. The relative consumption rate based on dry leaf mass (RCR_{dm}), the efficiency of conversion of ingested food to larval biomass (ECI), and the relative larval growth rate (RGR) were calculated. The following formulae were used:

- RCR_{dm} = (initial dry leaf mass – final dry leaf mass) / initial larval mass, in mg/mg/hr;

- ECI = (final dry larval mass – initial dry larval mass) / (final dry leaf mass – initial dry leaf mass), in mg/mg;
- RGR = $\log_e$(final larval mass) – $\log_e$(initial larval mass) / time (in hours), in mg/mg/hr.

Initial dry leaf and larval masses were calculated from regression equations obtained by weighing fresh and dry samples of 30 mature leaves and 20 larvae. Samples were dried at 60°C for 24 h. More individuals were used for consumption and food utilization evaluation but their behaviour was not recorded. A total of 73 fourth and 74 fifth instar larvae were used for RCR_{dm} calculations; 66 fourth and 65 fifth instar larvae were used for ECI calculations and 69 fourth and 69 fifth instar larvae were used for RGR calculations.

2.3.3.2. Behavioural traits

Videos were analyzed with The Observer® (Noldus, The Observer, version 5.0.31). This software is designed to analyze individuals' activities and behaviours. We labelled the insects' activities as *feeding*, *moving* and *pausing*. *Feeding* represents an insect actually chewing the leaf. *Moving* represents a larva moving on or off the leaf. *Pausing* represent time spent inactive. We did not consider inactivity as *resting* time for two reasons. First, resting time is usually defined as the time spent inactive after a meal. In the present experiment, we considered any break in feeding or moving as a pause, so this cannot be considered as resting time in its usual meaning. Second, our observation time had an approximate duration of 60 minutes. The actual resting period of individuals was usually not finished by the time the video was stopped. We calculated: 1) the proportion of the 1-hour observation time allocated to each activity; 2) the frequency of each activity during that time; and 3) the mean duration of each activity, calculated by divided the total duration of each activity by the frequency of occurrence of that activity.

2.3.4. Statistical analysis

Statistical computations were performed using the JMP 5.1 statistical package. To analyze the consequences of the different factors on caterpillar behaviour, multiple analyses of variance examined the effects of larval instar, rearing diet, observation leaf as well as interactions between them, on the time budget, frequency and mean duration of feeding, moving and pauses. Another model examined the effects of larval instar, rearing diet, observation leaf as well as interactions between them on relative consumption rate, food conversion efficiency and relative growth rate of the insects. Rank transformations were applied to all data sets that did not meet normality and homoscedasticity assumptions. When the model indicated a significant effect, differences were identified by performing Tukey-Kramer or t-tests, according to the number of groups compared.

Table I — Experimental design. Each observation is a combination of the insects' instar, rearing diet and observation leaf. Abbreviations for the combinations of rearing diet, observation leaf and instar are in bold characters.

Instar		4	4	5	5
	Observation leaf / Rearing diet	Aspen (A)	S. Maple (S)	Aspen (A)	S. Maple (S)
	Aspen (A)	**AA4** n = 10	**AS4** n = 10	**AA5** n =10	**AS5** n = 15
	Mixed (M)	**MA4** n = 8	**MS4** n = 7	**MA5** n = 15	**MS5** n = 11

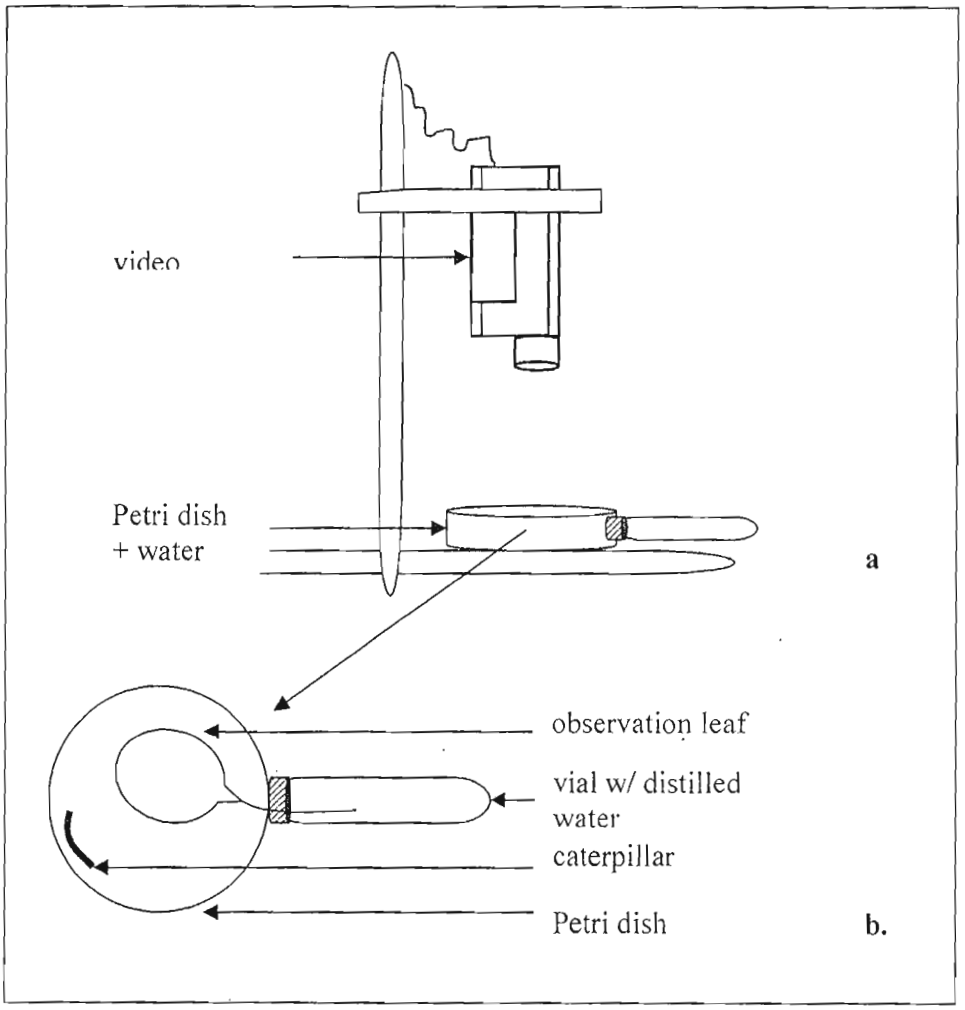

Figure 1.1 — Observation set-up from a a) side and b) top view

2.4. RESULT

2.4.1. General feeding patterns

Forest tent caterpillar larvae exhibit two distinct feeding patterns depending on host species.

In general, they feed more continuously on their primary host, trembling aspen, compared to the secondary one, sugar maple. Two typical patterns are illustrated on figure 1.2. The individual on trembling aspen spent over 25 minutes feeding continuously while the insect on sugar maple spent a maximum of 5 consecutive minutes feeding. For the latter, feeding was often interrupted by moving periods.

The way forest tent caterpillars generally behaved is also reflected by the way the leaves end up being eaten. As shown on figure 1.3, larvae tend to eat the sugar maple leaves in a scattered pattern by eating it at several locations along its edge, whereas for trembling aspen, consumption was often found at one single location of the leaf (fig 1.3).

2.4.2. Time budget

The model indicates that the proportions of time allocated to feeding, moving and pausing were all three significantly affected by the *observation leaf* factor alone (table II). Feeding time was an average of 1,5 times higher on trembling aspen (42,6±3,19 % [mean ± standard error]) than sugar maple (27,87±3,23 %), moving time was an average of almost 2,5 times higher on sugar maple (50,39±3,99 %) than trembling aspen (20,35±3,94 %) and pausing time was an average of 1,7 times higher on trembling aspen (36,75±3,49 %) than sugar maple (21,68±3.53 %).

As illustrated on fig. 1.4, the proportion of time allocated to feeding did not differ between individuals observed on sugar maple or aspen when they had been reared on a mixed diet. This was the case for both 4^{th} and 5^{th} instars (t-test; $p > 0,05$). However, when they had been reared on aspen, both 4^{th} (t-test; $p = 0,040$) and 5^{th} (t-test; $p = 0,036$) instars spent significantly more time feeding on aspen than on sugar maple (4^{th}

instar reared on trembling aspen and observed on: trembling aspen = 64±6,45 %, sugar maple = 33,2±6,45 % ; 5th instar reared on trembling aspen and observed on: trembling aspen = 30,4±6,45 %, sugar maple = 16,67±5,27 %).

On average, 4th instars spent twice as much time moving on sugar maple compared to aspen leaves. Fifth instars spent three times more time moving on sugar maple (illustrated on fig. 1.4).

Our model revealed a significant interaction between the *instar* and *rearing diet* factors for the proportion of time allocated to feeding and pauses (table II). Regardless of the host plant, 4th instars reared on an aspen diet spent significantly more time feeding than the ones reared on a mixed diet (t-test: $t = 2,61$; $p = 0,0134$), whereas 5th instars reared on aspen spent significantly less time feeding (t-test: $t = -3,69$; $p = 0,0006$) and more time in pause (t-test: $t = 2,66$; $p = 0,0125$) than the ones reared on a mixed diet.

2.4.3. Frequency of activities

The frequency of feeding and moving activities was significantly affected by the observation leaf (table III; fig. 1.5). Regardless of their instar or rearing diet, insects observed on sugar maple had more than twice as many feeding events (t-test: $t = -5,99$; $p < 0,0001$) as the ones observed on aspen. They also moved significantly more often ($t = -5,38$; $p < 0,0001$) when observed on sugar maple compared to aspen. However, this difference seems to be attenuated when individuals are reared on a mixed compared to an aspen diet (table III: significant interaction between rearing and observation leaves). This is particularly the case for 5th instar individuals whose feeding and moving frequencies did not differ between MA and MS diets (fig. 1.5).

2.4.4. Mean duration of activities

The mean duration of feeding bouts and pauses was significantly affected by the type of leaf on which the insects were observed (table IV). In general, larvae had

significantly longer feeding periods on aspen compared to sugar maple (fig 1.6). They also had longer pauses, although this difference was not significant (fig 1.6).

In addition, the model shows a significant interaction between the *instar* and *rearing diet* factors (table IV). Regardless of the leaf they were observed on, 4^{th} instar individuals reared on aspen had significantly longer feeding periods than 5^{th} instar individuals reared on the same diet (fig 1.6; t-test: t = 2,05; p = 0,0472). When reared on a mixed diet however, they had significantly shorter feeding periods (fig 1.6; t-test: t = -2,29; p = 0,0275), and significantly longer pauses than 5^{th} instar individuals (fig 1.6; t-test: t = 2,47; p = 0,0197).

2.4.5. Consumption rate

The relative consumption rates of fresh and dry foliage were proportionally equivalent, hence only the data for dry foliage consumption (RCR_{dm}) is presented in this paper.

During the 1-hour period of observation, 4^{th} instar larvae had a higher consumption rate than 5^{th} instar larvae (4^{th} instars: 0,0812 ± 0,0061 mg/mg/hr, 5^{th} instars: 0,0554 ± 0,0057mg/mg/hr; t-test: t = 2,75; p = 0,007). In particular, AS5 individuals which had the lowest consumption rate among all groups, decreased consumption of dry leaf material by a 2,65 fold compared to AS4 individuals (AS4: 0,0806 ± 0,0117mg/mg/hr; AS5: 0,0304 ± 0,0093mg/mg/hr).

The relative consumption rate of larvae over 24 hours was affected by the *observation leaf* factor alone (table V). Regardless of their instar or rearing diet, the larvae fed almost 1.25 times faster on aspen than on sugar maple during the 24-hour follow-up (trembling aspen: 0,0147±0,0009 mg/mg/hr; sugar maple: 0,0117±0.0008 mg/mg/hr).

2.4.6. Food conversion efficiency and relative growth rate over 24 hours.

Both efficiency of conversion of ingested food and relative growth rate were strongly affected by the leaf the insects were on (table VI). Insects fed aspen during

24 hours following the 1-hour observation period, were more efficient in converting that food than sugar maple (fig. 1.9). Accordingly, their relative growth rate was significantly higher on aspen (fig. 1.10). In fact, the mean ECI and RGR values were negative for insects on sugar maple (fig 1.9 and fig. 1.10).

Our model also revealed an effect of the *rearing diet* × *observation leaf* interaction (table VI) on the ECI and RGR variables. As shown on figures 1.9 and 1.10, insects observed on aspen tend to be more efficient in converting food when they have been reared on aspen before. Insects observed on sugar maple show a similar tendency and are more efficient in converting food when they have been reared on a mixed diet before. However, Tukey-Kramer comparisons did not identify these differences as significant.

Table II – Multi-Factor ANOVAs report for the effect of larval instar, rearing diet and observation leaf on the proportion of time allocated to feeding, moving and pauses by *Malacosoma disstria* larvae in a 1-hour period of observation.

	Source of variation	*df*	MS	F	p
% feeding	Instar	1	261,8404	0,5801	0,4486
	Rearing diet	1	2,1286	0,0047	0,9454
	Observation leaf	1	4749,3570	10,5219	**0,0017**
	Instar × Rear. diet	1	7878,7578	17,4549	**< 0,0001**
	Instar × Obs. leaf	1	300,7634	0,6663	0,4168
	Rear. diet × Obs. leaf	1	637,1460	1,4116	0,2384
	Rear. diet × Obs. leaf × Instar	1	527,1850	1,1679	0,2832
	Error	78	451,38		
% moving	Instar	1	627,35	1,3882	0,2423
	Rearing diet	1	822,23	1,8195	0,1813
	Observation leaf	1	11842,75	26,2062	**< 0,0001**
	Instar × Rear. diet	1	617,06	1,3655	0,2462
	Instar × Obs. leaf	1	1262,65	2,7941	0,0986
	Rear. diet × Obs. leaf	1	79,72	0,1764	0,6756
	Rear. diet × Obs. leaf × Instar	1	52,12	0,1153	0,7351
	Error	78	451,91		
% pausing	Instar	1	208,978	0,4196	0,5190
	Rearing diet	1	79,108	0,1588	0,6913
	Observation leaf	1	3064,173	6,1527	**0,0153**
	Instar × Rear. diet	1	6447,897	12,9471	**0,0006**
	Instar × Obs. leaf	1	1834,141	3,6829	0,0586
	Rear. diet × Obs. leaf	1	1482,329	2,9765	0,0884
	Rear. diet × Obs. leaf × Instar	1	1466,640	2,9449	0,0901
	Error	78	498,02		

Table III – Multi-Factor ANOVAs report for the effect of larval instar, rearing diet and observation leaf on the frequency of feeding, moving and pauses by *Malacosoma disstria* larvae in a 1-hour period of observation. The frequency represents the number of times each activity was observed.

	Source of variation	*df*	MS	F	p
feeding	Instar	1	678,00	1,6086	0,2084
	Rearing diet	1	502,87	1,1931	0,2780
	Observation leaf	1	15505,81	36,7897	**< 0,0001**
	Instar × Rear. diet	1	920,88	2,1849	0,1433
	Instar × Obs. leaf	1	2,41	0,0057	0,9399
	Rear. diet × Obs. leaf	1	3004,11	7,1277	**0,0092**
	Rear. diet × Obs. leaf × Instar	1	196,63	0,4665	0,4966
	Error	78	421,47		
moving	Instar	1	456,96	1,0403	0,3109
	Rearing diet	1	585,32	1,3325	0,2518
	Observation leaf	1	13232,06	30,1227	**< 0,0001**
	Instar × Rear. diet	1	1218,28	2,7734	0,0998
	Instar × Obs. leaf	1	29,49	0,0671	0,7962
	Rear. diet × Obs. leaf	1	3867,02	8,8032	**0,0040**
	Rear. diet × Obs. leaf × Instar	1	45,10	0,1027	0,7495
	Error	78	439,27		
pausing	Instar	1	77,225	0,1409	0,7084
	Rearing diet	1	60,816	0,1110	0,7399
	Observation leaf	1	896,229	1,6353	0,2047
	Instar × Rear. diet	1	5103,222	9,3114	**0,0031**
	Instar × Obs. leaf	1	1156,243	2,1097	0,1503
	Rear. diet × Obs. leaf	1	4098,561	7,4783	**0,0077**
	Rear. diet × Obs. leaf × Instar	1	183,091	0,3341	0,5649
	Error	78	548,06		

Table IV – Multi-Factor ANOVAs report for the effect of larval instar, rearing diet and observation leaf on the mean duration (in seconds) of feeding, moving and pausing activities of *Malacosoma disstria* larvae in a 1-hour period of observation. The mean duration is calculated by divided the total duration of each activity by the frequency of occurrence of that activity.

	Source of variation	*df*	MS	F	ρ
feeding	Instar	1	1,30	0,0039	0,9506
	Rearing diet	1	309,53	0,9164	0,3414
	Observation leaf	1	16553,61	49,0105	**< 0,0001**
	Instar × Rear. diet	1	3149,74	9,3255	**0,0031**
	Instar × Obs. leaf	1	827,43	2,4498	0,1216
	Rear. diet × Obs. leaf	1	1566,49	4,6379	**0,0344**
	Rear. diet × Obs. leaf × Instar	1	113,16	0,3350	0,5644
	Error	78	337,76		
moving	Instar	1	1730,503	2,9320	0,0908
	Rearing diet	1	563,563	0,9548	0,3315
	Observation leaf	1	924,534	1,5664	0,2145
	Instar × Rear. diet	1	94,314	0,1598	0,6904
	Instar × Obs. leaf	1	996,151	1,6878	0,1977
	Rear. diet × Obs. leaf	1	2247,699	3,8083	0,0546
	Rear. diet × Obs. leaf × Instar	1	45,095	0,0764	0,7830
	Error	78	590,214		
pausing	Instar	1	481,354	0,8941	0,3473
	Rearing diet	1	416,550	0,7737	0,3818
	Observation leaf	1	3270,535	6,0746	**0,0159**
	Instar × Rear. diet	1	4043,401	7,5102	**0,0076**
	Instar × Obs. leaf	1	1952,490	3,6265	0,0606
	Rear. diet × Obs. leaf	1	64,803	0,1204	0,7296
	Rear. diet × Obs. leaf × Instar	1	633,848	1,1773	0,2812
	Error	78	538,39		

Table V – Multi-Factor ANOVAs reports for the effect of larval instar, rearing diet and observation leaf on the relative consumption rate (RCR_{dm}) of *Malacosoma disstria* larvae in 1 hour and 24 hours.

	Source of variation	*df*	MS	F	ρ
1 hour	Instar	1	0,02228	9,5520	**0,0024**
	Rearing diet	1	0,01302	5,5821	**0,0196**
	Observation leaf	1	0,00440	1,8858	0,1719
	Instar × Rear. diet	1	0,00375	1,6062	0,2072
	Instar × Obs. leaf	1	0,00229	0,9835	0,3231
	Rear. diet × Obs. leaf	1	0,00107	0,4571	0,5001
	Rear. diet × Obs. leaf × Instar	1	0,01631	6,9900	**0,0092**
	Error	137	0,00233		
24 hours	Instar	1	780,99	0,4675	0,4953
	Rearing diet	1	233,84	0,1400	0,7089
	Observation leaf	1	24053,10	14,3982	**0,0002**
	Instar × Rear. diet	1	190,03	0,1138	0,7364
	Instar × Obs. leaf	1	1027,03	0,6148	0,4343
	Rear. diet × Obs. leaf	1	398,93	0,2388	0,6258
	Rear. diet × Obs. leaf × Instar	1	806,60	0,4828	0,4883
	Error	139	1670,56		

Table VI – Multi-Factor ANOVAs report for the effect of larval instar, rearing diet and observation leaf (24h follow-up) on the relative growth rate (top) and efficiency of conversion of ingested food (bottom) of *Malacosoma disstria* larvae over 24 hours.

	Source of variation	*df*	MS	F	ρ
RGR	Instar	1	3620,00	2,6939	0,1031
	Rearing diet	1	5721,82	4,2580	**0,0411**
	Observation leaf	1	88840,08	66,1127	**<0,0001**
	Instar × Rear. diet	1	1573,88	1,1712	0,2811
	Instar × Obs. leaf	1	2719,12	2,0235	0,1573
	Rear. diet × Obs. leaf	1	6893,07	5,1297	**0,0252**
	Rear. diet × Obs. leaf × Instar	1	1422,62	1,0587	0,3054
	Error	130	1343,8		
ECI	Instar	1	2588,31	3,1691	0,0775
	Rearing diet	1	5156,63	6,3137	**0,0133**
	Observation leaf	1	47750,69	58,4656	**<0,0001**
	Instar × Rear. diet	1	1970,53	2,4127	0,1229
	Instar × Obs. leaf	1	2102,01	2,5737	0,1112
	Rear. diet × Obs. leaf	1	4738,32	5,8016	**0,0175**
	Rear. diet × Obs. leaf × Instar	1	2114,42	2,5889	0,1102
	Error	123	816,7		

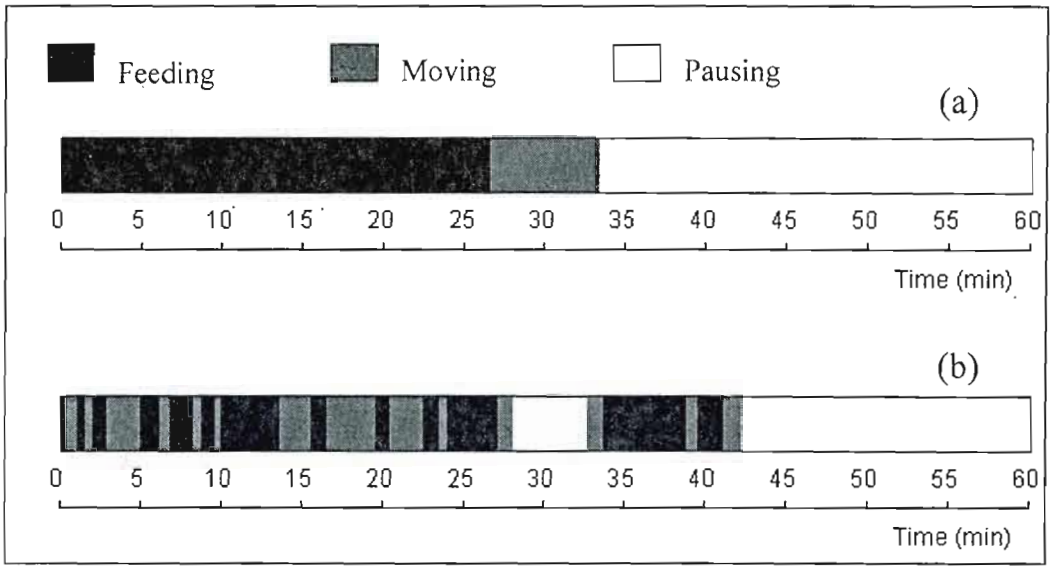

Figure 1.2 — Time line of the activities of two *Malacosoma disstria* larvae during a 1-hour period of observation. (a) Observation #30: 5th instar individual reared and observed on trembling aspen; (b) Observation #15: 4th instar individual reared on a mixed diet and observed on sugar maple.

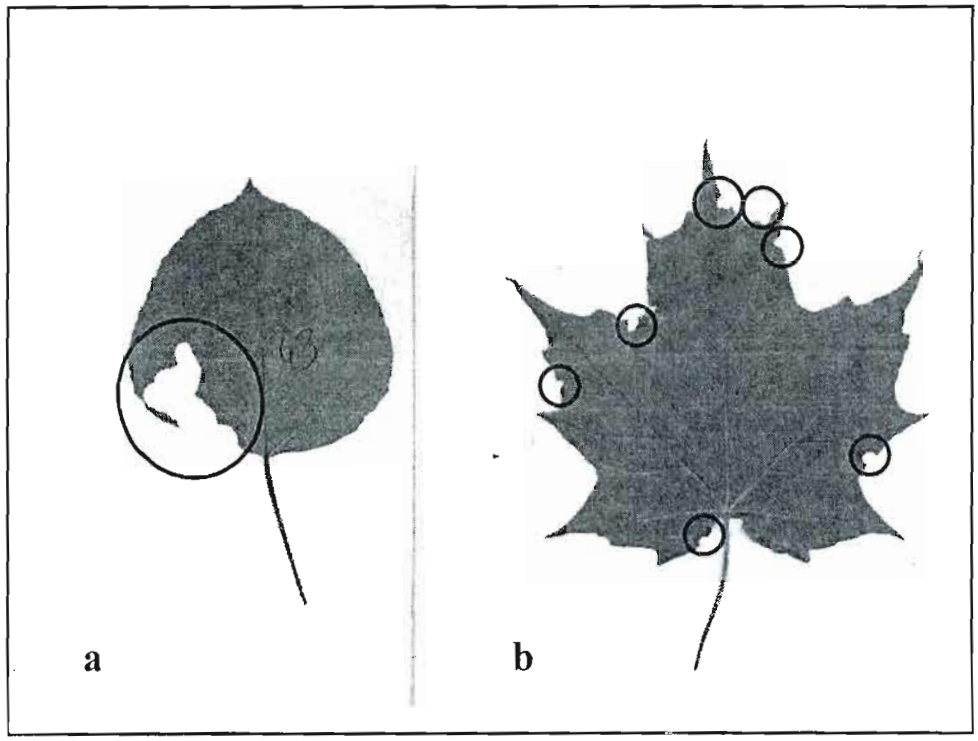

Figure 1.3 — Feeding pattern of two *Malacosoma disstria* larvae. (a) Observation #43: 5th instar individual reared on a mixed diet and observed on trembling aspen; (b) Observation #45: 4th instar individual reared on a mixed diet and observed on sugar maple. Pictures represent the scans of the leaves after the 1-hour observation period.

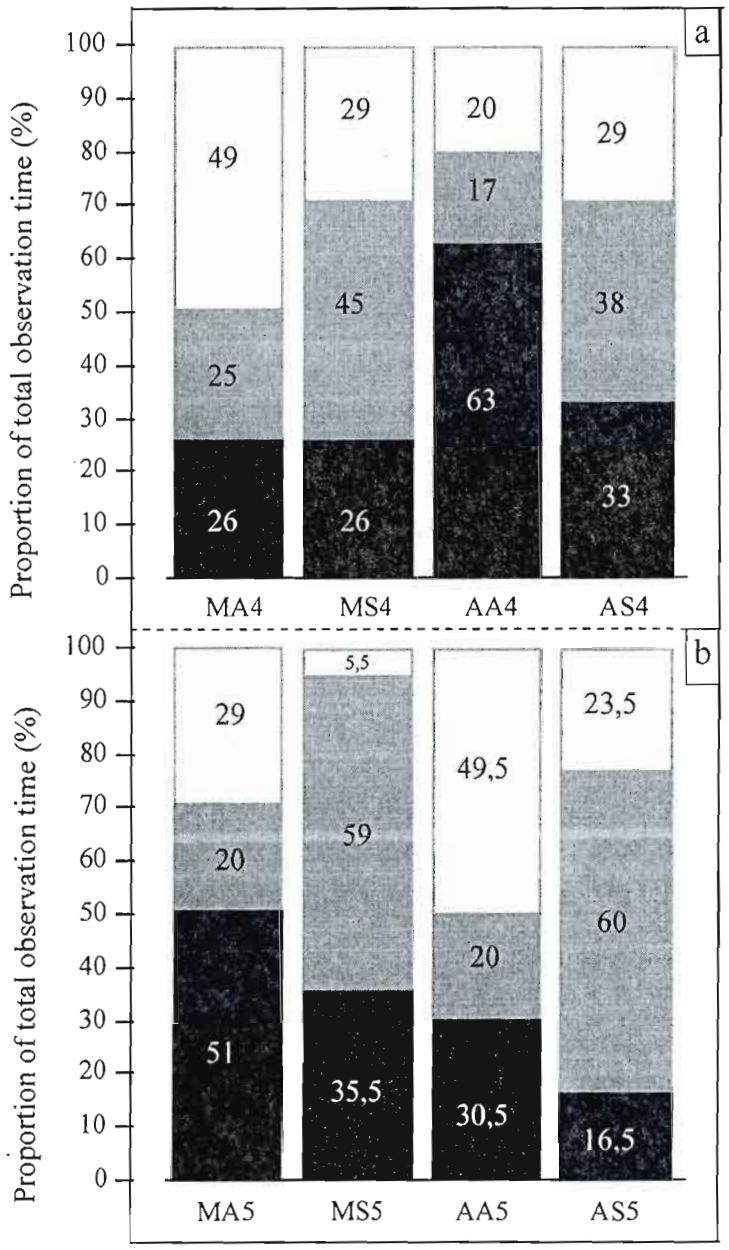

Figure 1.4 — Time allocation budget: proportion of 1-hour observation time spent feeding, moving and pausing for (a) 4th instars (n=35) and (b) 5th instars (n=51) of *Malacosoma disstria* larvae observed on trembling aspen and sugar maple. Figures represent the percentage of the total observation time. See Table I for treatments abbreviations description.

Feeding Moving Pausing

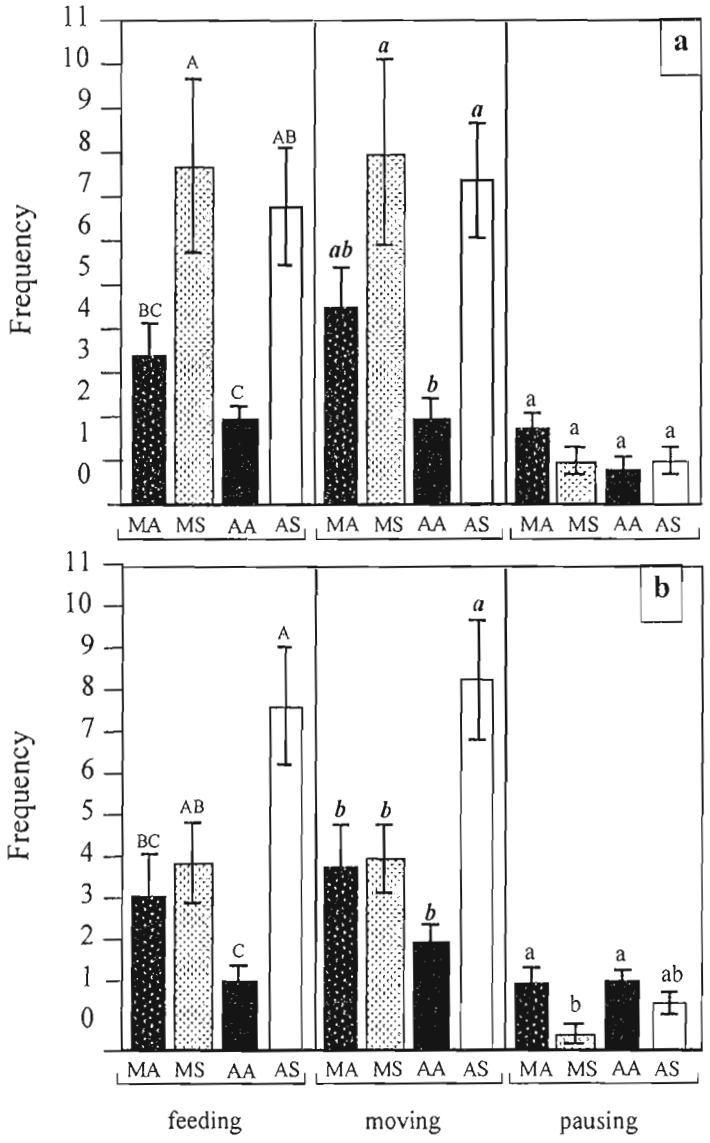

Figure 1.5 —Frequency of feeding, moving and pausing bouts for (a) 4th instars (n = 35) and (b) 5th instars (n=51) of *Malacosoma disstria* larvae observed on trembling aspen and sugar maple. The frequency represents the number of times each activity was displayed during the observation period. Within each activity, bars headed by letters that are not commonly shared are significantly different ($p < 0.05$, Tukey-Kramer test). Error bars represent *SE*. See Table I for treatments abbreviations description.

MA MS AA AS

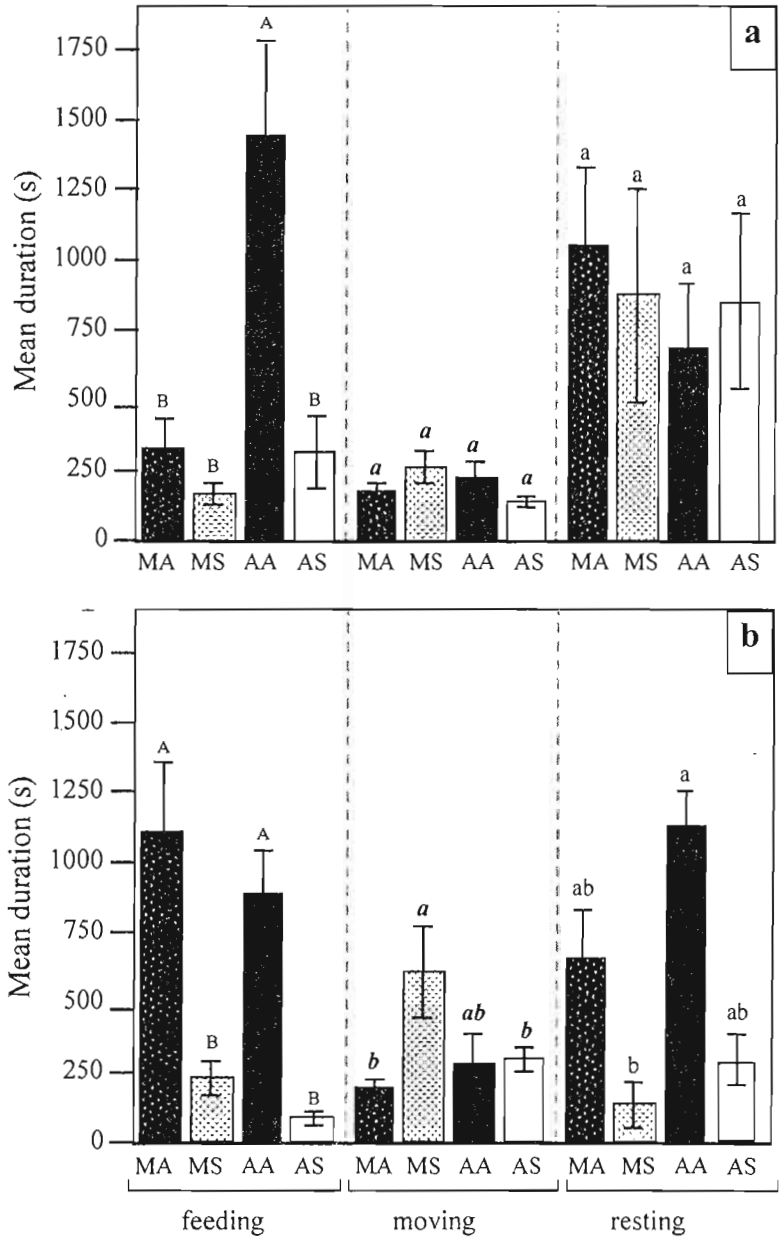

Figure 1.6 — Mean duration of feeding, moving and pausing bouts for 4th (a) and 5th instar (b) larvae of *Malacosoma disstria* observed on trembling aspen (n = 43) and sugar maple (n = 43). The mean duration is calculated by divided the total duration of each activity by the frequency of occurrence of that activity. Within each activity, bars headed by letters that are not commonly shared are significantly different ($p < 0.05$, Tukey-Kramer test). Error bars represent *SE*. See Table I for treatments abbreviations description.

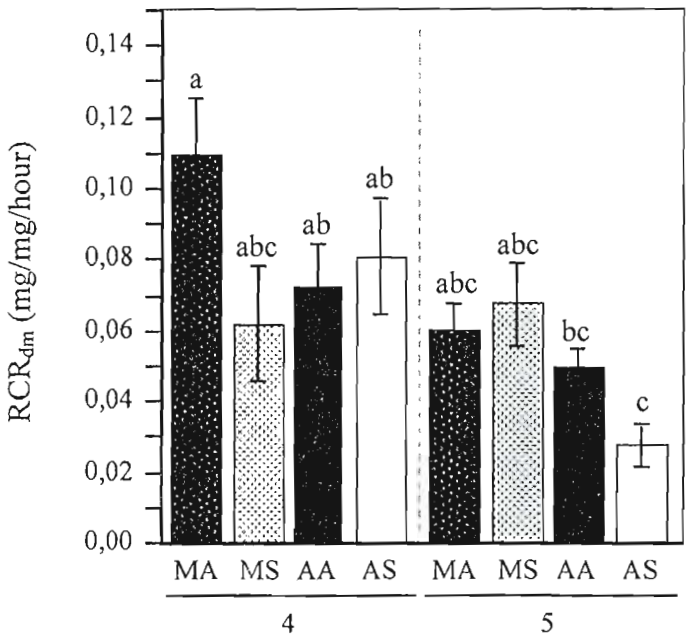

Figure 1.7 — Relative consumption rate (RCR) of dry foliage for larvae (4^{th} and 5^{th} instars) of *Malacosoma disstria* during the **1-hour** period of observation. Bars headed by letters that are not commonly shared are significantly different ($p < 0.05$, Tukey-Kramer test). Error bars represent *SE*. See Table I for treatments abbreviations description.

MA MS AA AS

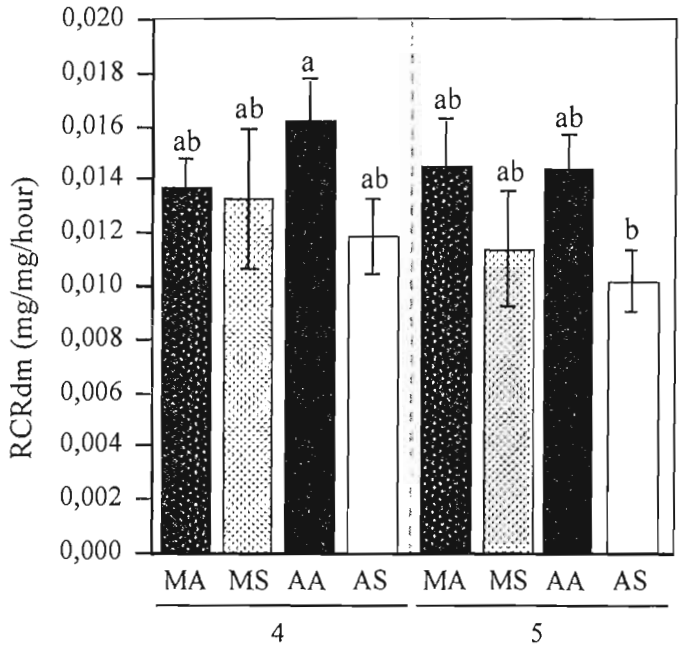

Figure 1.8 — Relative consumption rate (RCR) of dry foliage for 4th (top) and 5th instar larvae (bottom) of *Malacosoma disstria* in **24-hours**. Bars headed by letters that are not commonly shared are significantly different ($p < 0.05$, Tukey-Kramer test). Error bars represent *SE*. See Table I for treatments abbreviations description.
MA MS AA AS

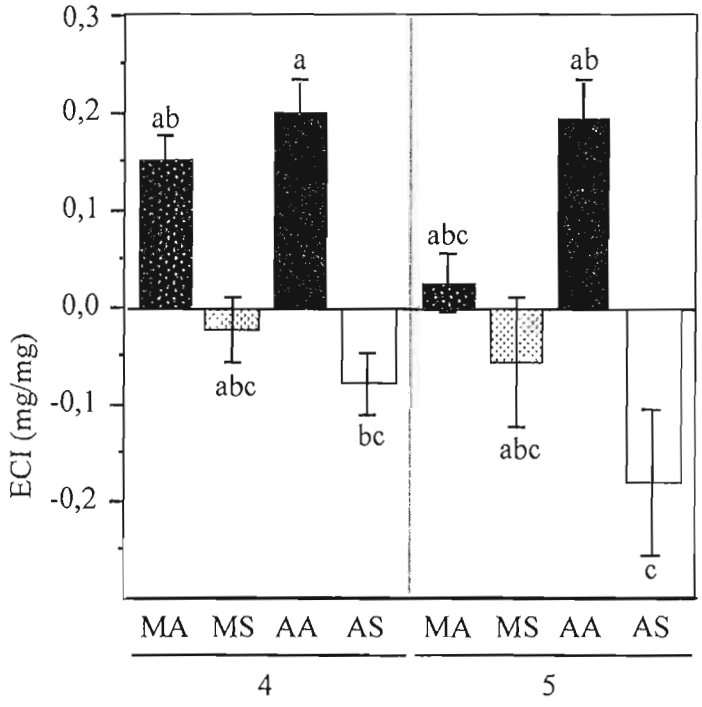

Figure 1.9 — Efficiency of conversion of ingested food (ECI) for 4th (left) and 5th instar larvae (right) of *Malacosoma disstria* in **24-hours**. Bars headed by letters that are not commonly shared are significantly different ($p < 0.05$, Tukey-Kramer test). Error bars represent *SE*.

MA MS AA AS

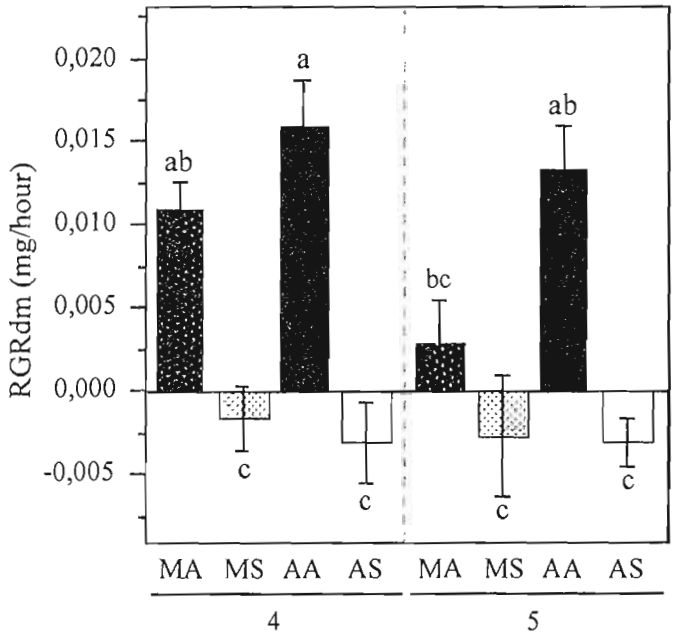

Figure 1.10 — Relative growth rate for 4th (left) and 5th instar larvae (right) of *Malacosoma disstria* in **24-hours**. Bars headed by letters that are not commonly shared are significantly different ($p < 0.05$, Tukey-Kramer test). Error bars represent *SE*.

MA MS AA AS

2.5. DISCUSSION

2.5.1. Effect of host species on caterpillars' behaviour

Forest tent caterpillars' behaviour seems to be primarily affected by the host leaf on which they are feeding. In presence of their primary host, trembling aspen, larvae tend to feed fewer times but for longer periods of time. On their secondary host, the insects feeding activity is much less continuous and interrupted by frequent moving bouts. However, we did not find striking differences in the time spent feeding or the amount of food ingested on the two hosts.

Trembling aspen leaves contain about twice as much soluble sugars as sugar maple (Fortin *et al.*, 1999, Panzuto, 2001). These sugars are known to stimulate feeding in phytophagous insects (Bernays and Chapman, 1994; Nicol *et al.* 1997). Feeding stimulants have also been found in other *Populus* species leaf surface (Lin *et al.*, 1998). In addition, sugar maple leaves contain more phenolic compounds (defense compounds) than trembling aspen leaves (Lorenzetti, 1993; Fortin *et al.* 1999). These are known to dissuade phytophagous insects from feeding (Bernays and Chapman, 1994; Nicol *et al.* 1997; Fortin *et al.*, 1999; Panzuto, 2001). We suggest that the chemical input caterpillars receive from their food is strong enough to initiate continuous feeding on aspen but not on sugar maple due to the chemical composition of the leaves.

Food quality influences searching behaviour in insects (Bell, 1990). As a consequence of the lower quality of sugar maple leaves, we suggest that forest tent caterpillar larvae adopt an increasing search strategy, as described in sawflies by Kause *et al.* (1999). In presence of a lower quality food, it should be advantageous to increase search for a better or at least more stimulating food source (Schultz, 1983; Bell, 1990). In our particular case, this strategy is illustrated by a process of repeated sampling and rejection by the larvae feeding on sugar maple leaves (illustrated on figures 1.2 and 1.3). Through this strategy, the larvae are able to ingest approximately

the same amount of food as on trembling aspen, suggesting that they possibly sample and reject until they reach satiety (Simpson, 1995; Simpson, Raubenheimer et Chambers, 1995).

As described by Begon *et al.* (1990), increased movement is synonymous of an increased energy loss. Such energy loss may have contributed to the significantly lower ECI and growth rates observed for individuals that had been followed on sugar maple for 24 hours. In fact, not only were the ECI and growth rates lower on sugar maple, but they were in average always negative on that host, meaning that most larvae feeding on sugar maple lost weight over a 24 hours period of time. The caterpillars in this study did not get any benefit from feeding on sugar maple. This certainly is the consequence of a poor leaf quality combined with an increased energy loss and we suspect the origin of the caterpillars used in this study to be partly responsible for this outcome. Indeed, sugar maple is a typically eastern species and consequently not part of Alberta's forest tent caterpillars hosts. Variation in the suitability of host tree species for geographically discrete populations of forest tent caterpillar has already been found (Parry and Goyer, 2004). As an exemple, forest tent caterpillars from Louisiana had small pupal mass and poor survival on sugar maple, whereas other Northern populations from Manitoba or Michigan were not so affected by a sugar maple diet (Parry and Goyer, 2004).

In addition to energy loss, predation risk may be increased by movement of forest tent caterpillars. As described for *Manduca sexta* and *Uresiphita reversalis* (Bernays, 1997), increasing locomotion could induce an increased risk of being seen by mammal and avian predators. However, because of their hairy cuticle, risks of avian predation are minimized in late instar *M. disstria* larvae (Heinrich, 1979, Fitzgerald, 1995). More importantly however, forest tent caterpillars are frequently attacked by entomophagous insect species (Fitzgerald, 1995). A relationship between their moving activity and the risk of predation by entomophagous insects should therefore be investigated.

We observe two very different feeding patterns on leaves of trembling aspen and sugar maple, as illustrated on figure 1.3. Larvae frequently made several small holes on sugar maple leaves and one much bigger hole on trembling aspen leaves. Similar feeding patterns were found for *Spodoptera littoralis* larvae (Lepidoptera: Noctuidae) on damaged versus intact tomato leaves (Barker *et al.* 1995). That study and the present one provide evidence that the observed sampling and rejection process is a behavioural pattern normally exhibited by larvae encountering less acceptable foliage. The changed distribution of feeding damage that results on such foliage may provide a quick method of assessing leaf palatability in studies of plant-insect relationship.

It is known that predators (Heinrich, 1979; Heinrich and Collins, 1983) use physical changes in damaged leaves to locate insect hosts. Risks from intensified attack by predators associated with damaged leaves may therefore be different on trembling aspen versus sugar maple leaves. Nevertheless and as previously stated, the unpalatable characteristic of forest tent caterpillars could protect them against such predation risk increase. Parasitoids use chemical cues to locate insect hosts (Vinson, 1975; Faeth, 1985) and the effect of differential physical damage on the quantity and identity of chemicals released could be investigated.

2.5.2. Effect of feeding experience and larval stadium on caterpillars' behaviour.

Our results indicated that the feeding behaviour of *M. disstria* larvae was modified according to the diet they had experienced before. However, these behavioural modifications were not the same for 4^{th} or 5^{th} instar larvae.

Fifth instars that had never been in contact with sugar maple previously to their observation (AS5) exhibited a more exploratory behaviour than the ones reared on a diet containing sugar maple (MS5). They had about twice as many feeding and moving bouts, which were in average half shorter. They also had a significantly lower consumption rate during the hour of observation.

The feeding experience of fourth instar individuals did not significantly affect the way they behaved in presence of sugar maple. The time allocation budget, frequency and duration of activities or consumption rate did not differ between MS4 and AS4 individuals.

We suggest that a previous contact with the lower quality diet may have induced habituation in 5th instar larvae (de Boer and Hanson, 1984; Dethier, 1988; Bernays and Weiss, 1996). Habituation is a decrease of aversion to a plant that was first deterrent, but following repeated contact or a period of forced feeding, became palatable. Such a decrease in negative response may involve habituation to deterrents or an increased ability to process xenobiotics (Lindroth, 1991; Bernays and Weiss, 1996). This process has been demonstrated in polyphagous lepidopterans (e.g. *Mamestra brassicae*; Jermy *et al.*, 1982) in attempts to identify mechanisms facilitating larger feeding breadth. However, the fact that this was only expressed by 5th instar individuals suggests that the expression of the habituation mechanism might require a particular physiological state of the insect. In several lepidopteran larvae, the activity of mixed-function oxidases, allowing to detoxify toxic phytochemicals, increases with age (Brattsten, 1979). In gypsy moth, a polyphagous lepidopteran, midgut pH increases with larval age, providing greater ability to detoxify secondary compounds (Schultz and Lechowicz, 1986). It is therefore possible that in *M. disstria*, 5th instars are more susceptible to accept a food high in secondary compounds than 4th instars, due to an increased detoxifying ability.

As suggested by Bernays and Weiss (1984), the habituation process might be expected to parallel post-ingestive enzymatic changes, so that food that has become less deterrent also becomes less noxious. In the present study, we did not find any clear evidence for this phenomenon because although the ECI and RGR were higher on MS5 versus AS5, this different was not statistically significant.

We found more behavioural differences between 4th and 5th instar individuals on the homogeneous AA treatment. While 5th instars spent almost 50% of their time

in pause and only 30,5 % of their time feeding , 4th instars spent only 20% of their time in pause and more than 60% of their time feeding. This result is consistent with results obtained for 4th versus 5th instar larvae of *Helicoverpa armigera*, another herbivorous lepidopteran (Raubenheimer and Barton Browne, 2000). This study revealed a significant reduction in the amount of feeding time from the 4th to 5th larval instar. In both *H. armigera* and *M. disstria*, the 5th instar usually corresponds to the last instar and therefore, to the period when larvae prepare to the final moult to the pupal stage. This could possibly be reflected by a transitional period of low-commitment to nutrient intake (Raubenheimer and Barton Browne, 2000). The higher consumption rates of AA4 versus AA5 individuals would support this possibility; however, since this difference was not significant, we cannot definitely make this conclusion.

2.6. CONCLUSION

Forest tent caterpillar larvae increased searching time on sugar maple, behaved differently according to their age, and were affected by the food they had experienced before.

These results suggest that a polyphagous species like the forest tent caterpillar and possibly other polyphagous insects, do not forage on different species in equivalent ways. It seems that they respond to changes in leaf palatability by changes in their feeding behaviour. It shows that ecologists need to consider the possibility of changes in pests' behaviour and in the distribution of damage to plant material, not just overall consumption rates, when assessing herbivore insects' responses to different forest species and when developing pest management strategies (Barker et al., 1995; Johnson et Zalucki, 2005).

This study also demonstrates the importance of considering ontogeny in behavioural studies. Differences between 4^{th} and 5^{th} instar feeding patterns indicates the appropriateness of measuring a variety of behavioural parameters at different larval stages before inferring general conclusion for a species. It would therefore be relevant to analyze individuals feeding patterns before the 4^{th} instar, when forest tent caterpillars are still gregarious foragers.

Although we have shown that the forest tent caterpillar shows host-specific feeding patterns on two plant species in the Québec region, it is possible to find different patterns on the same hosts in other North-American regions. Indeed, we might expect varying responses according to different combinations of the insect and host species origin (Parry and Goyer 2004). A comparison of feeding patterns across North-American regions may give valuable information on the adaptative value of the plasticity in the feeding behaviour of the insect.

Finally, since *Malacosoma disstria* is a highly generalist species, it would be quite interesting to observe its behaviour on other host species in order to see if the same or other behavioural patterns are found.

NOTE : Cette page explique le lien direct entre les chapitres II et III.

En 2005, le comportement alimentaire de livrées des forêts se nourrissant de peuplier faux-tremble (*Populus tremuloides*) a été comparé à son comportement sur de l'érable à sucre (*Acer saccharum*). Cette expérience est relatée au chapitre II et révèle deux patrons d'alimentation distincts selon l'hôte que les chenilles consomment. Afin d'élargir notre connaissance du comportement alimentaire de la livrée des forêts sur ses différents hôtes naturels, le comportement de l'insecte à été observé l'année suivante sur du bouleau blanc (*Betula papyrifera*) et du chêne rouge (*Quercus rubra)*. L'objectif de cette deuxième année d'expérimentation qui est relatée au chapitre III était donc de voir si les patrons trouvés l'année précédente pouvaient être retrouvés sur d'autres hôtes ou alors si les insectes présentaient un tout autre comportement. Il s'agissait également, lors de cette deuxième série d'observation, de tenter de faire des liens entre les caractéristiques communes à ces hôtes, les préférences de l'insecte pour ces différents hôtes et les comportements qui y sont associés. Les méthodes d'observation étaient similaires à celles de 2005 : des enregistrements vidéos d'une heure de temps analysés par le logiciel The Observer®, développé pour des analyses comportementales.

CHAPITRE III – FEEDING BEHAVIOUR OF THE FOREST TENT CATERPILLAR, *MALACOSOMA DISSTRIA* HÜBNER ON WHITE BIRCH (*BETULA PAPIRYFERA*) AND RED OAK (*QUERCUS RUBRA*) LEAVES

Elsa Etilé and Yves Mauffette

3.1. ABSTRACT

The feeding behaviour of the forest tent caterpillar (*Malacosoma disstria*) has previously been observed on trembling aspen and sugar maple leaves and a different feeding pattern was found on each host. The objective of the present study was to investigate on the possibility to find similar or new feeding patterns on these two other hosts: white birch (*Betula papiryfera*) and red oak (*Quercus rubra*) and eventually, to make a link between hosts characteristics and insects feeding patterns. Through video-recorded observations, we evaluated and compared the foraging behaviours (feeding, movement and pauses) of *M. disstria* larvae feeding on leaves of white birch and red oak. The caterpillars increased movement and reduced pauses on red oak compared to white birch. Their feeding activity was much more intermittent on red oak. These results are very similar to what was found on trembling aspen and sugar maple. The insects behaved in the same fashion on red oak and sugar maple and in another fashion on white birch and trembling aspen. The link between repetitive feeding patterns and life history traits of plants are discussed.

Key words: feeding behaviour, activity budget, polyphagy, Lepidoptera, *Malacosoma disstria*, *Betula papiryfera*, *Quercus rubra*.

3.2. INTRODUCTION

Consumption, utilization and allocation of food are essential components of all animals' lives and the selection pressures acting upon these three components are the most common causes of the evolution of different life-histories (Slansky and Rodriguez, 1987). In order to understand the diversity of life-histories exhibited by arthropods, it is essential to approach their nutritional ecology by integrating biochemical, physiological but also behavioural information (Singer and Bernays, 2003)

Contrary to the earlier view that organisms are passive energy partitioners and transducers (Slansky, 1982a), it is now obvious that feeding is a complex behaviour that is closely regulated by both endogenous and exogenous factors (Slansky and Rodriguez, 1987; Bernays and Chapman, 1994; Simpson, 1995). Arthropods show considerably flexible feeding behaviours, many of which have been shown to be adaptive (e.g. Slansky and Scriber, 1985; Barton Browne and Raubenheimer, 2003).

The forest tent caterpillar (*Malacosoma disstria* Hbn., Lepidoptera: Lasiocampidae) is a generalist lepidopteran (Fitzgerald, 1995). It can reach epidemic numbers and cause severe damage to North-American deciduous forests (Fitzgerald, 1995; Nicol *et al*, 1997). In Québec, severe defoliations have most often been reported on trembling aspen (*Populus tremuloides*) and sugar maple (*Acer saccharum*) but larvae damages have been observed on many other plant species (Ressources Naturelles et Faune Québec, 2008; Fitzgerald, 1995) including white birch (*Betula papyrifera*) and red oak (*Quercus rubra*).

The highly generalist trait of *Malacosoma disstria* makes it a good species to study the impact of variability in food characteristics on the evolution of plasticity in feeding behaviours.

In chapter II, the feeding behaviour of forest tent caterpillars was compared on trembling aspen versus sugar maple. The results have shown that the larvae exhibit

two distinct feeding behaviours according to the host they feed on and that these behaviours are also influenced by other endogenous and exogenous factors.

In the present experiment, we focus on the influence of the host species by attempting to identify forest tent caterpillars feeding behaviour on two other hosts: white birch (*Betula papyrifera*) and red oak (*Quercus rubra).* We investigate on the possibility to find similar or new feeding patterns on these two other hosts and try to make links between hosts characteristics, insects' preferences and the feeding behaviours exhibited.

3.3. MATERIAL AND METHODS

Laboratory experiments were carried out at the Mont-St-Hilaire research center (45.3°N, 73.0°W) in Québec, Canada, from May to June 2006.

3.3.1. Insects rearing

Forest tent caterpillar egg bands were collected in April 2006 at Havelock, Québec, and stored at 4°C until the first white birch leaf buds appeared at the end of April 2006. From April to May, a total of five egg bands were sterilized in 5.4% sodium hypochlorite for 1 minute and 30 seconds, washed in cold tap water for 5 minutes and then rinsed in 0.06% sodium hypochlorite (Grisdale, 1985). Each band was placed in a numbered plastic container lined with wet paper towel and wax paper and covered with a net. The containers were kept in a growth chamber at 24°C, 50% relative humidity, and under a 16L:8D photoperiod.

Between 50 and 150 individuals emerged from each egg mass, after 3 to 5 days. Because of their natural gregarious behaviour, insects were reared in groups of 200-300 indiviuals for the first three instars and 50 individuals for the last instars.

Caterpillars were fed *ad libitum* with freshly cut leaves. They were given a mixed diet of white birch (*Betula papyrifera*) and red oak (*Quercus rubra*). Mixing was ensured by alternating white birch and red oak every two days. Leaf dehydration was prevented by inserting petioles into florist vials filled with distilled water. Leaves were selected between 3 and 6m high, from a sample of 20 mature trees (DBH > 10 cm) within a perimeter of 200 meters around the research center on the St-Hilaire Hill (45°33'08" N - 73°09'50" O). The site is part of a mixed temperate forest.

3.3.2. Behavioural observations set-up

Freshly molted 5th instars were transferred from the rearing containers to a new container and allowed to feed for 48 to 72 hours. Individuals used for

observation were then randomly picked among them, put into individual Petri dishes and deprived of food during 12 hours before observation time. A total of 24 fifth instar larvae were used for behavioural observations.

A Petri dish was used as observation chamber. A 2mm-diameter hole was pierced into its wall. A florist vial was glued in front so that a leaf petiole could pass through and be maintained into distilled water. Before each observation, the leaf was cut, weighed and scanned (Scanner HP Scanjet 4070 Photosmart) for surface area calculations (UTHSCSA Image Tool for Windows®, version 3.00).

After the food deprivation period, caterpillars were measured with a caliper (body length and head capsule widths), weighed with an electronic scale (Sartorius H51; precision: 0.01mg), then placed into one observation chamber.

A digital camera (Sony Handycam, DCR-DVD201) recorded caterpillars' behaviour. The video started once the insect initiated feeding in order to ensure that stress related to manipulation was over by the time the observation started.

An observation consisted in a one-hour video record of one caterpillar feeding on a leaf of either white birch (WB) or red oak (RO). Twelve caterpillars were observed on each from May, 25 to June, 7, 2006.

3.3.3. Data collected

Videos were analyzed with The Observer® (Noldus, The Observer, version 5.0.31). This software is designed to analyze individuals' activities and behaviours. We labelled the insects' activities as *feeding*, *moving* and *pausing*. *Feeding* represents an insect actually chewing the leaf. *Moving* represents a larva moving on or off the leaf. *Pauses* represent time spent inactive. We calculated: 1) the proportion of the hour allocated to each activity; 2) the frequency of each activity in the 1-hour period; and 3) the mean duration of each activity.

3.3.4. Statistical analysis

Statistical computations were performed using the JMP 5.1 statistical package. T-tests examined the effects of the species eaten by the insects on the time budget, frequency and mean duration of feeding, moving and pauses.

3.4. RESULTS AND DISCUSSION

Forest tent caterpillars moved about three times more and paused three times less on red oak compared to white birch. However, the proportion of time they allocated to feeding did not differ between the two hosts (fig. 2.1).

As illustrated on fig. 2.2, the larvae fed almost two times more often on red oak. They also moved more often on that host, although the difference was not statistically significant. The frequency of pauses did not vary between the two hosts ($p = 0,73$).

The larvae had significantly longer moving periods and shorter pauses on red oak compared to white birch (fig. 2.3). The mean duration of feeding bouts did not differ between the two species.

In light of these results, we suggest that forest tent caterpillars show plasticity in their feeding behaviour, similarly to what was observed on trembling aspen versus sugar maple leaves (chapter II). In presence of red oak, similar to sugar maple, the caterpillars tend to have a more intermittent feeding activity. This is expressed by a higher moving time, more frequent feeding and moving bouts, as well as significantly longer moving bouts on red oak compared to white birch.

This suggests that characteristics commonly shared by red oak and sugar maple and by trembling aspen and white birch could possibly be responsible for similar behavioural responses from the insects.

There have been several attempts to relate herbivore food preferences to life history characteristics of plants. Cates and Orians (1975) and Reader and Southwood (1981) presented evidence that early successional plants tend to be more palatable to generalist herbivores than those of later successional stages (Cates and Orians 1975; Reader and Southwood, 1981; Edwards *et al.*, 1986). Trembling aspen and white birch are both early successional plants whereas sugar maple and red oak are generally regarded as late successional or climax species (Rook, 2002). These

common characters are possibly linked to forest tent caterpillars feeding behaviour. Further investigation is needed before drawing clear relationships here.

Species of *Populus* and *Betula* produce a flush of early leaves in the spring followed by a series of individual late leaves through the summer (indeterminate growth), but species like sugar maple or red oak normally produce only one spring flush of foliage (determinate growth) (Clausen and Kozlowski, 1965; Lechowicz, 1984). This difference in the timing of leaf flush confers leaves different chemical and physical properties. It has often been reported that new leaves are of higher quality (more nitrogen, fewer secondary compounds, reduced toughness, etc.) than old leaves, so that they are preferred by herbivores (Feeny, 1970; Hunter and Lechowizc, 1992). If new trembling aspen and white birch leaves develop continuously throughout the growing season, they will be in greater proportion on these trees than on red oak or sugar maple at the same moment in time. Although this difference in foliage development is interesting to notice, a detailed analysis of the effect of this factor on herbivores behaviour would be necessary before concluding in that way.

In conclusion, we suggest that further than being responsible for feeding preferences in insects, the life history traits of plants can possibly cause differential behavioural responses from them. Further experimentation is definitely needed that will isolate traits commonly shared by plants and relate them to feeding behaviour in herbivorous insects.

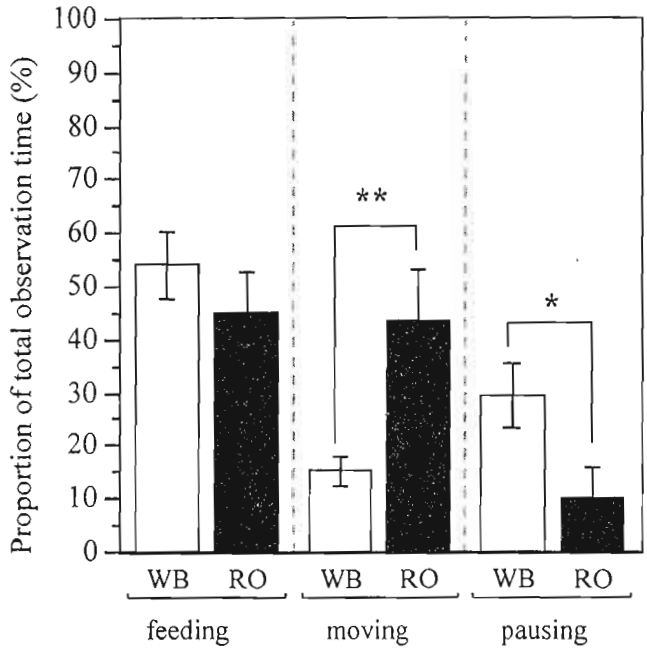

Figure 2.1 — Time allocation budget: proportion of 1-hour observation time spent feeding, moving and pausing for 5th instar larvae of *Malacosoma disstria* observed on white birch (n = 12) and red oak (n = 12). Error bars represent *SE*. (*) indicates a significant difference: (*$\rho < 0{,}05$; ** $\rho < 0{,}01$; *** $\rho < 0{,}0001$).

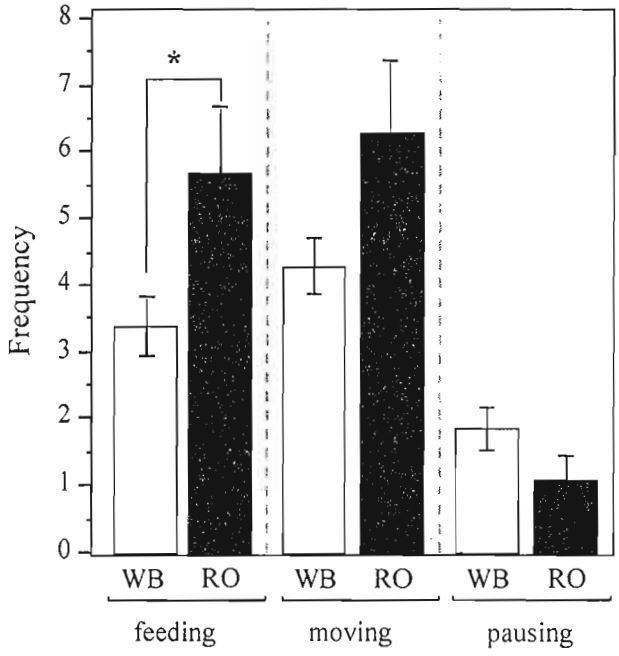

Figure 2.2 — Frequency of feeding bouts, moving bouts and pauses for 5th instar individuals of *Malacosoma disstria* observed on white birch or red oak during 1 hour. The frequency represents the number of times each activity was displayed during the observation period. Error bars represent *SE*. (*) indicates a significant difference (*ρ < 0,05; ** ρ < 0,01; *** ρ < 0,0001)

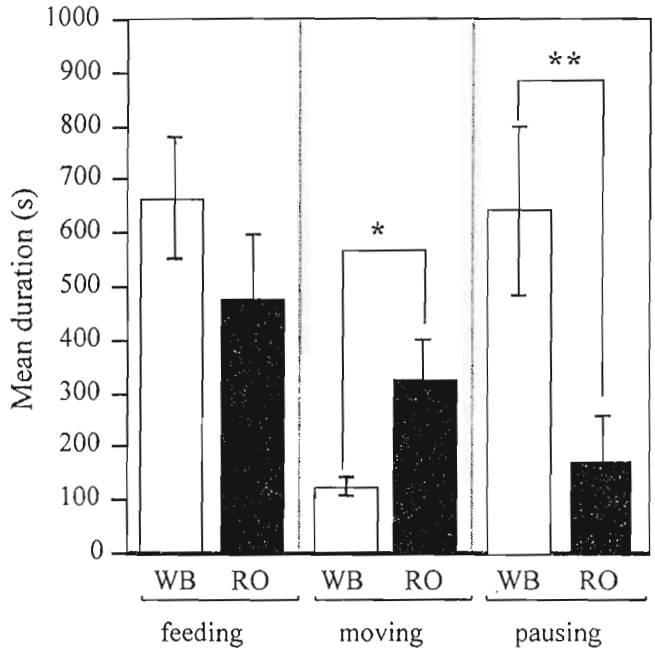

Figure 2.3 — Mean duration of feeding bouts, moving bouts and pauses for 5th instar larvae of *Malacosoma disstria* observed on white birch and red oak during 1 hour. The mean duration is calculated by divided the total duration of each activity by the frequency of occurrence of that activity. Error bars represent *SE*. (*) indicates a significant difference: *$\rho < 0{,}05$; ** $\rho < 0{,}01$; *** $\rho < 0{,}0001$.

Table VII – ANOVA report for the effect of the "observation leaf" on the time budget, frequency and mean duration of each activity of *M. disstria* larvae observed during 1 hour.

	Source of variation	*df*	MS	F	ρ
Time budget	Feeding	1, 22	20,17	0,393	0,537
	Moving	1, 22	352,67	9,73	**0,005**
	Pausing	1, 22	216	5,09	**0,034**
Frequency	Feeding	1, 22	192,67	4,43	**0,047**
	Moving	1, 22	80,67	1,66	0,211
	Pausing	1, 22	24	0,469	0,501
Mean duration	Feeding	1, 22	104,17	2,19	0,153
	Moving	1, 22	266,67	6,64	**0,017**
	Pausing	1, 22	308,17	8,05	**0,0096**

CONCLUSION GÉNÉRALE

Le comportement alimentaire de larves de livrée des forêts a été comparé sur quatre de ses hôtes naturels. Il en ressort que le patron d'alimentation de l'insecte n'est pas fixe mais qu'au contraire, il est flexible et particulier sur chaque hôte. Cependant, nous avons pu faire ressortir deux patrons généraux similaires selon la préférence de l'insecte pour son hôte. En effet, sur des hôtes préférentiels comme le peuplier faux-tremble (*Populus tremuloides*) et le bouleau blanc (*Betula papiryfera*), la consommation de l'insecte est continue et ciblée, alors que sur des hôtes secondaires comme l'érable à sucre (*Acer saccharum*) et le chêne rouge (*Quercus rubra*), il semble adopter un comportement plus exploratoire ce qui résulte en une alimentation plus discontinue et entrecoupée d'épisodes de déplacement plus fréquents.

Notre étude suggère que l'information reçue lors de la consommation des feuilles est en partie responsable d'un changement de comportement de l'insecte. Cette observation pourrait s'expliquer par des différences dans la chimie foliaire des espèces considérées dans cette étude ; différences plusieurs fois rapportées entre l'érable à sucre et le peuplier faux-tremble. Par conséquent, au-delà de leur rôle dans la performance biologique des individus ou dans le choix d'un hôte par l'insecte (Fraenkel, 1959), les composés chimiques des plantes pourraient aussi être déterminants dans les mécanismes permettant aux espèces polyphages de moduler leur comportement face à l'hétérogénéité nutritionnelle à laquelle ils sont confrontés. Une telle flexibilité comportementale pourrait donc être un élément déterminant du succès de ces espèces polyphages. La livrée des forêts est un bon exemple d'espèce polyphage particulièrement efficace : elle a une très haute capacité épidémique et est l'un des lépidoptères les plus répandus en Amérique du Nord (Fitzgerald, 1995).

En plus des caractéristiques de l'hôte sur lequel l'insecte s'alimente, il est apparu que l'âge de la larve ainsi que son expérience alimentaire pouvaient influencer son comportement de manière significative. Ceci confirme que les facteurs nutritifs à

son comportement de manière significative. Ceci confirme que les facteurs nutritifs à eux seuls ne peuvent expliquer les variations importantes qui existent dans différents écosystèmes au niveau des préférences alimentaires des individus (Singer et Bernays, 2003).

Les causes et conséquences d'un mode de vie polyphage dépendent du comportement alimentaire des individus (Bernays et Graham, 1988; Singer et Bernays, 2003). La valeur des informations recueillies dans cette étude confirme l'importance de se pencher sur l'aspect comportemental des individus dans les relations plantes-insectes afin de comprendre les stratégies adaptatives ayant mené aux choix alimentaires que l'on constate aujourd'hui ainsi que leur importance dans la dynamique des populations, communautés et écosystèmes.

Bien que cette étude apporte des informations de valeur sur le caractère polyphage des livrées des forêts, des observations en nature seraient également nécessaires afin de clarifier comment des facteurs tels que l'équilibre nutritionnel, la dilution des toxines ou encore l'évitement du risque jouent leur rôle en nature. Par ailleurs, nos résultats ont été obtenus pour un seul système, celui de la livrée des forêts. Le fait que la tendance observée dans cette étude soit typique de la plupart des lépidoptères polyphages est loin d'être sûr. Il serait donc très pertinent de reproduire ce genre d'observations comportementales sur d'autres espèces polyphages afin de déterminer si des patrons comportementaux communs ressortent, mais aussi afin d'avoir une idée plus précise de la valeur de cette plasticité comportementale dans un mode vie généraliste. À la lumière des résultats obtenus dans les présentes expériences, il apparaît important que ces futures études tiennent compte des facteurs qui peuvent avoir une incidence sur ces comportements tels que le stade de développement des individus, leur expérience alimentaire, les contraintes imposées par les ennemis ou encore les traits d'histoire de vie des plantes hôtes. L'emplacement géographique des populations de livrée et la distribution

géographique de leurs plantes hôtes s'avèrent également être des éléments à ne pas négliger.

Ce projet permet par ailleurs d'affirmer qu'il est risqué de présumer que les insectes généralistes se comportent de la même façon sur leurs différents hôtes. Cette information peut être de grande valeur lorsqu'on en vient à développer des moyens de contrôle de ces insectes, lorsqu'ils sont considérés comme nuisibles. La connaissance des différents comportements que peuvent exhiber les individus dans leur milieu naturel pourrait donc permettre de développer des méthodes de contrôle plus appropriées, et peut-être même plus efficaces.

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